Small mammal dynamics within a natural river corridor, Fiume Tagliamento NE Italy

Iordan, Francesca

Awarding institution:
King's College London

Small mammal dynamics within a natural river corridor,

Fiume Tagliamento NE Italy

A thesis submitted for the degree of Doctor of Philosophy

Francesca Iordan
Department of Geography
King's College London

Thesis abstract

This PhD thesis explores the effects of spatial arrangements of riparian landscape elements and food resources on community and population dynamics of small mammals within a braided section of the River Tagliamento in Italy.

The main research questions addressed were: (1) Which variables affect small mammal diversity on river islands? (2) Do small mammal populations inhabiting river islands differ in their life histories compared to riparian forest populations (the 'island syndrome')? (3) Is there a difference in the spatial behaviour of small mammals inhabiting the riparian forest compared to those on the islands?

Three rodent species were used as focal species to address these questions: *Apodemus sylvaticus*, *A. flavicollis* and *A. agrarius*. The expectations were that small mammal dynamics did not fit completely island biogeography and life-history models developed for oceanic islands because islands in the present study are characterised by a low degree of isolation from the surroundings, by an ephemeral nature due to periodical flooding and by a low availability of food resources for small mammals.

The main findings confirm these expectations, with the three species only partially following the predictions both at community and population ecology levels. Of the three species, *A. sylvaticus* was the most insular and more closely followed the predictions, in particular that of the island syndrome. Small mammal diversity on the islands was affected by island area, by the flooding dynamics and by resource availability. Finally, home ranges of *A. agrarius* were much larger on the islands than in the riparian forest. The findings suggest that river islands in the study area are a lower-quality habitat, partly due to their ephemeral nature, but the presence of habitat heterogeneity introduced by the islands allows for the rich community of small mammals to segregate, hence increasing species diversity at a landscape level.

Acknowledgments

This thesis would have never been written if I had not met Laura Bonesi at the University of Trieste. She has always been a mentor for me and convinced me that if I wanted to start a PhD, I should move to the UK.

This is how everything started; a couple of years travelling across the whole UK to volunteer on different projects in ecology and applying to different PhD positions and finally finding Rob Francis at King's, studying the Friulian River Tagliamento…in London. Therefore, I would like to say one million "thank you's" to my supervisors; Rob Francis for giving me the opportunity to do this work and to Laura Bonesi for her great support throughout the thesis, the corrections of the thesis and all the scientific work I have done up to now.

I would also like to thank all the volunteers and students who made the fieldwork fun. Special thanks to Marko Zupan, Elena Fabi, Brigitte Zoller, Luca Dorigo, Annapaola Monte and also to Lukas Polednik and Katerina Polednikova for putting up with me in the last two weeks before submission, last year.

Several people helped me with constructive criticism: John Gurnell, Sara Churchfield, Paola Ganis and Lukas Indermaur. All of them took time to talk to me or to read my work or part of my work. A huge thank to goes to Marco Girardello who spent several hours to advise me about statistics. I enjoyed working with him during the last days before the submission of the thesis corrections. I would also to like to thank scientists that discussed with me aspects of the thesis: Robert Long, William Zielinski, Peter Apps and Luca Lapini.

Finally I would like to thank all my friends at 11A Sharon Gardens E9 7RX, in particular Jeremy Bourdon and Sophie Smiles, who always supported me and made my time in London really, really special. Also the guys of THERION Research Group, in particular Cristina Rieppi, deserve a thanks, because they believed in me and pushed me to keep on going also in the very dark periods before re-submission. Thanks also to my sister Marianna and my brother Matteo, who suffered my irritability throughout the last months and fed me and washed the dishes in the very last days before submission of the thesis corrections.

This thesis is dedicated to my blond Kari, the son of the River and to his cute dimples and to my mother and my father, for their infinite love, support, vitality and strength.

Table of contents

Chapter 1 - Literature review 12
1.1 Introduction 12
1.2 What is an island?.. 15
1.3 The Theory of Island Biogeography.. 15
1.4 Habitat islands 17
1.5 What is a landscape? 20
1.6 Rivers as landscapes 21
1.7 Life histories of oceanic and continental island vertebrates..................... 24
1.7.1 The island rule and the island syndrome 24
1.7.2 Predator release on islands.. 26
1.7.3 Competitive release/niche expansion on islands 27
1.7.4 Resource availability on islands 30
1.8 Life histories traits of habitat island vertebrates...................................... 31
1.9 Thesis structure and aims 35
Chapter 2 35
Chapter 3 - Research question N. 1... 35
Chapter 4 - Research question N. 2... 36
Chapter 5 - Research question N. 3... 37
Chapter 6 38
Chapter 7 38
1.10 References 39

Chapter 2 - Overview of the River Tagliamento study system, mammal diversity and sampling protocols 45
2.1 Study system..45
2.1.1 The active tract of the Tagliamento 45
The ephemeral nature of islands in the active tract.......................................47
Vegetation composition of islands 50
2.1.2 The riparian forest of the Tagliamento 50
2.2 Description of the study area and selected sites 51
2.3 The pilot study: choosing the focal species 56
2.4 Sampling protocol 60
2.4.1 Small mammals..60
Genetic verification of small mammal species for doubtful cases.................63
2.4.2 Carnivores..65
2.5 Mammal species recorded on the Tagliamento 66
2.6 Focal species...68
2.6.1 Apodemus flavicollis: general biology 68
2.6.2 Apodemus sylvaticus: general biology 69
2.6.3 Apodemus agrarius: general biology 70
2.6.4 Martes foina: general biology 71
2.7 References 73
Chapter 3 - Influence of scale-dependent factors in regulating small mammal assemblages in a semi-natural riparian landscape.. 77
3.1 Introduction 78
3.2 Methods..81
3.2.1 Study area and species under study 81

3.2.2 Small mammal trapping and estimation of small mammal diversity 82

3.2.3 Explanatory variables describing islands attributes 84

Biotic and abiotic variables 84

3.2.4 Spatial variables 86

3.2.5 Statistical methods 87

Causal interaction between variables 87

Construction of the a priori model 89

3.3 Results 92

3.3.1 Small mammal density and diversity...92

3.3.2 Effects of patch scale and landscape scale variables on small mammal diversity 93

Correlation between the input variables..93

3.3.3 Causal interactions between variables 94

3.4 Discussion..97

3.4.1 Small mammal responses to patch scale variables 98

3.4.2 Small mammal responses to landscape scale variables 101

3.4.3 The combined effect of patch and landscape scale analysis 104

3.5 References 107

Chapter 4 - The island syndrome of a rodent riparian community 112

4.1 Introduction 113

4.2 Methods..117

4.2.1 Study area 117

4.2.2 Rodent sampling 118

4.2.3 Food resources analysis 120

4.2.4 Data analysis 120

4.3 Results 124

4.3.1 Life history variation and island syndrome gradients 124

Population densities 124

Proportion of adults 127

Reproductive output 129

Weights 130

4.3.2 Food resources analysis 133

4.4 Discussion 134

4.4.1 Density compensation in the Apodemus community of Tagliamento river islands 134

4.4.2 Quantification of the timespan to develop island syndrome traits 138

4.4.3 Conclusions 140

4.5 References 142

Appendix 4.1 146

Chapter 5 - Home ranges of male *Apodemus agrarius* in a riparian landscape: consequences of resource availability and edge effects 147

5.1 Introduction 148

5.2 Methods 152

5.2.1 Study site 152

5.2.2 Radio tracking 154

5.2.3 Home range estimation 156

5.2.4 Factors affecting home range characteristics 156

Apodemus spp. population densities 156

Estimation of resource availability 157

Edge effects 158

5.2.5 Statistical analyses 158

5.3 Results 161

5.3.1 Home range characteristics in the two habitats 161

5.3.2 Population densities of *Apodemus* spp. in the two habitats 167

5.3.3 Food resources in the two habitats 169

5.3.4 Distance of the centre of the home range from habitat edges 169

5.3.5 Factors affecting home range and core area size 170

5.4 Discussion 175

5.4.1 Factors that affect home range size 175

5.4.2 Factors that affect core area size, number and distance 180

5.4.3 Conclusions 181

5.5 References 183

Appendix 5.1 189

Chapter 6 - Habitat use of the stone marten (*Martes foina*) in a natural riparian landscape 190

6.1 Introduction 191

6.2 Methods 194

6.2.1 Study area 194

6.2.2 Distribution data 196

6.2.3 Detecting the presence of carnivores 197

6.2.4 Study design 199
6.2.5 Explanatory variables 200
Spatial variables 200
Food abundance variables 201
6.2.6 Statistical analysis 202
Model building and selection 203
6.3 Results 205
6.3.1 Distribution data 205
6.3.2 Explanatory variables 206
Spatial variables 206
Food abundance variables 209
6.3.3 Model selection 211
6.4 Discussion 213
6.4.1 The use of scent stations as a way of detecting carnivores 213
6.4.2 Factors affecting M. foina use of the Tagliamento floodplain 214
6.4.3 Conclusions 216
6.5 References 217
Chapter 7 - General discussion 221
7.1 Reduced species diversity on river islands 222
7.2 Over-representation of generalist species on islands 229
7.3 Larger home ranges of *A. agrarius* on islands 232
7.4 Reduction of predator species 235
7.5 Changes in life history traits 237

7.5.1 Increased densities on islands 237

7.5.2 Decreased reproductive output on islands 237

7.5.3 Inter-specific relationships 239

7.5.4 Increased survival on islands 241

7.5.5 Data collection for estimating life histories 242

7.6 Changes in body size 244

7.7 Conclusions 247

7.7.1 The Tagliamento as model ecosystem of European importance 249

Chapter 1 - Literature review

1.1 Introduction

The last two decades have shown a substantial shift in the focus of ecological studies to the landscape scale, due to increasing recognition that environmental issues need to be addressed at broad spatial and temporal scales (Francis 2009; Wiens 2002). This is particularly true for river systems, which are highly connected spatially and temporally and have strong hierarchical linkages that ensure that broad-scale changes are rapidly cascaded through the system (Habersack 2000; Wiens 2002). This thesis will explore a relatively neglected are of landscape ecological research, which is the relationship between riparian landscape mosaics and small mammal community and population dynamics.

Riparian corridors, as a dynamic mosaic of spatial elements and ecological processes arrayed hierarchically fit comfortably within the framework of landscape ecology, a discipline which deals with the study of the interaction between spatial patterns and ecological processes in the context of spatial heterogeneity across a range of scales (Turner 1998). Riparian corridors, as defined by Ward and Tockner (2001) correspond to the surface areas composed of interacting terrestrial and aquatic units that are directly influenced by the river (i.e., aquatic habitats, floodplain surface, and riparian zone). They are amongst the most bio-diverse terrestrial landscapes in the world and represent important functional buffers between aquatic and terrestrial areas (Naiman et al. 1993), especially for animals (Lehmkuhl et al. 2008; Meier et al. 2005; Robichaud et al. 2002; Shirley 2006).

Due to centuries of engineering works to regulate streams, most rivers in the world are by now far from being natural, even though river planning trends changed recently, with increasing emphasis on ecologically orientated river management (Lake et al. 2007). In Europe almost all large Alpine rivers were ‘trained’ during the first half of the 20th century (Dynesius and Nilsson 1994), sometime before the science of river ecology developed (Petts et al. 1989).

One of the rivers that have maintained natural morphology, hydrological dynamism and an intact riparian zone in Europe is the River Tagliamento in North-Eastern Italy (Tockner et al. 2003; Ward et al. 1999). The riparian zone is characterised by the presence of a wide riparian forest bordering the banks and of river islands along several reaches: these two main structural characteristics of the Tagliamento allow the formulation of the central question of this thesis: ‘Do the population and community dynamics of small mammal species on river islands fit within the frameworks of island biogeography and landscape ecology?’. Key principles of island biogeography and landscape ecology were tested within a dynamic, heterogeneous environment represented by a braided section of the River Tagliamento. Such considerations are fundamental to inform landscape conservation, management and restoration efforts in degraded river corridors across the world.

In the next sections of this chapter some of the main principles and processes that constitute the framework of island biogeography and landscape ecology are presented. The successive chapters (3, 4, 5 and 6) have their own literature review and some of these processes are discussed more in detail depending on the subjects covered in each chapter.

The conceptual framework of this thesis encompasses the theory of island biogeography that primarily explains community ecology level patterns, and theories aimed at explaining life-history differences in island vertebrates (including differences in home ranges). As the physical system where the study took place is not that of oceanic islands where these theories have been developed, it is important that the way in which the riparian landscape differs from that of oceanic islands is carefully considered. Landscape ecology does provide a framework to help us quantify these differences. The section below considers the theories that underpin this thesis, explains how the questions asked have originated, and describes the fundamentals of landscape ecology to provide a framework for the comparison of the riverine landscape with that of oceanic islands.

1.2 What is an island?

The term ‘island’ can be used to describe any piece of land surrounded by a body of water. In geological and biogeographical terms two broad types of islands can be distinguished: *continental* and *oceanic*. The former are located over the continental shelf and in the past were connected to the mainland. The latter are found over the oceanic plate and have never been connected to continental land masses (Whittaker 1998). A third island type commonly referred to in biogeography is *mainland islands*. They are ‘islands of habitat’ in a ‘sea’ or matrix of surrounding distinct land use (MacArthur et al. 1972).

In the context of this thesis the islands of the River Tagliamento are considered as habitat islands and defined as isolated patches of riparian woodland within a braided river corridor surrounded by gravel in conditions of low flow and water in conditions of high flow (Gurnell and Petts 2002; Tockner et al. 2003).

1.3 The Theory of Island Biogeography

Islands are variable in their physical characteristics with each island differing for example in shape, size, degree of isolation, vegetation cover, geography, etc. Colonisation opportunities and extinction risks of species vary concurrently with these characteristics, with features such as island area and distance from the mainland having a particularly strong effect (Mayr 1967). Consequently, islands often encompass unique biotic assemblages and thus have served as 'natural laboratories' for studying theories and testing hypotheses in ecology (Whittaker 1998).

The *Theory of Island Biogeography* (MacArthur and Wilson 1967) was developed to describe the mechanisms regulating the assemblages of species on oceanic islands. Seawater provides a significant barrier to the dispersal of most terrestrial species, thus the theory predicts that number of species on islands is set by an equilibrium between distance from mainland-dependent immigration and island area-dependent extinction: therefore the theory predicts that the smaller and more isolated an island is, the lower the species richness it will support (Figure 1.1). In detail, species extinction rate on islands is determined by the birth and the death rate of those species on that island and its carrying capacity. The immigration rate is determined by the distance between islands, the rate at which dispersing propagules are produced, the survivorship, and distance travelled during dispersal.

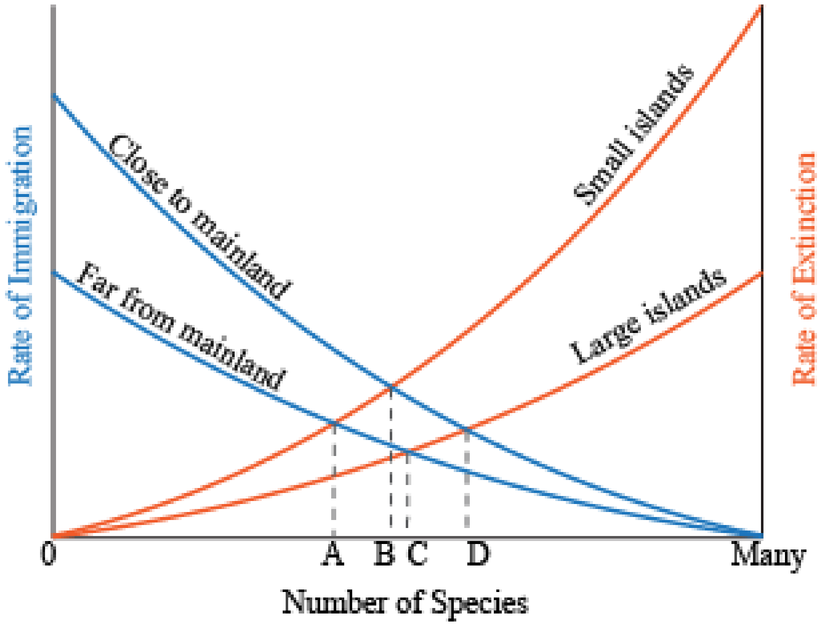


Figure 1.1 MacArthur and Wilson's model: from left to right, the immigration line decreased while the extinction line increased. In other words, as the number of species on the island increased, the number of extinctions increased and the number of successful immigrations decreased. The intersection of these two lines identified the equilibrium state. The island will reach equilibrium when extinction rates equal immigration rates,. that is the A, B, C, and D in the graph , which are different depending on size and distance. SOURCE: Modified by F. Iordan after Brown and Lomolino (1998).

This complex relationship between immigration and extinction processes operating on islands, often results in the occurrence of a depauperate flora and fauna with respect to mainland communities. Newly colonising species on islands may find themselves in the absence of a normal suite of competitors and predators and in vastly different habitat to that from which they came, therefore undergoing different selective pressures.

1.4 Habitat islands

The Theory of Island Biogeography became one of the foundations of landscape ecology (Forman and Godron 1981). In landscape ecology a 'habitat island' (or a habitat patch, used interchangeably in this thesis) is defined as, '*a spatially delimited portion of remnant habitat differing from its surroundings in nature or appearance*' (Forman and Godron 1981).

Over the years following the publication of the Theory of Island Biogeography, the idea that habitat islands are analogous to oceanic islands took root, becoming a central theme in conservation biology (e.g. Brown 1971; Debinski and Holt 2000; Saunders et al. 1991). Habitat island size and isolation, analogous to island size and isolation, became viewed as a primary determinant of species richness in habitat islands. Often these habitats islands are represented by grasslands and forests, 'ecologically' isolated by an inhospitable matrix of intensive agriculture, but not always. The term habitat islands may also be applied to many non-traditional 'islands', such as the peaks of mountains (Frey et al. 2007), isolated shrubs surrounded by grassland (Sanchez and Parmenter 2002), non-contiguous woodlands (Lomolino and Perault 2001) or remnant natural habitats inserted in an inhospitable sea of human activity (Mendenhall et al. 2014). This means that in biological terms we can consider as islands all small biotopes, far enough from a 'mainland' or isolated to such an extent that migratory movements or genetic exchanges with mainland populations are more difficult or even impossible.

Island biogeography was conceived to explain patterns of species richness and did not consider ecological attributes of species. True islands (i.e. oceanic and continental islands), as already pointed out, can be isolated simply as a function of their distance from a ‘source’ of new colonists; but the effective distance will vary between species, with some vagile species able to travel long distances to colonise new sites. The peculiarities in species richness, species diversity, morphology and life histories found on oceanic archipelagos result from their peculiar geological and evolutionary histories, that, furthermore, are extremely variable from case to case. Habitat islands such as forest remnants on the other hand, will generally have similar evolutionary histories to the mainland forest they have been isolated from. Moreover, ecological processes in forest remnants are in various ways critically influenced by direct interactions with remnant surroundings, whereas such interactions are negligible in oceanic islands (Haila 2002).

In terrestrial environments, isolating factors are complex: habitats and species are more or less isolated depending upon distance, climatic, geological, geomorphological and altitudinal factors, the permeability of the surrounding habitat matrix, the occurrence of habitat corridors and edge effects (Vogiatzakis and Griffiths 2008). The matrix in particular can significantly influence the distribution of species and populations in habitat islands and thus, over the years following the publication of the Island Biogeography Theory, the ecological properties of the matrix itself started to be considered in understanding the dynamics operating in different landscapes (Bender and Fahrig 2005; Kupfer et al. 2006; Ricketts 2001; Vandermeer and Carvajal 2001). Indeed, several studies revealed that species composition could change with habitat island isolation because species do differ in their abilities to cross the matrix between habitat islands (e.g. Pires et al. 2002; Prevedello et al. 2010).

Debinski et al. (2000) conducted a literature survey and canvassed the ecological community to identify experimental studies on terrestrial habitat islands and to determine whether consistent themes were emerging from these studies. They found that experiments with arthropods showed the best fit with theoretical expectations of greater species richness on larger habitat islands. Highly mobile taxa such as birds and mammals, early-successional plant species, long-lived species, and generalist predators did not respond in the 'expected' manner. Edge effects, interspecific competition mechanisms within habitat islands, and the spatial scale of the experiments were all put forward as possible explanations for these discrepancies.

Other factors that turned out to be significant in affecting the species richness and diversity of habitat islands are the variable age of the island (i.e. traits driving species distribution on young habitat islands can be different from those which have been fragmented for a longer time) (Vogiatzakis and Griffiths 2008), microhabitat variety within islands (MacArthur and Wilson 1967) and disturbance factors acting on the habitat island (i.e. disturbance by people, by livestock or even stochastich disturbance, Fox and Fox 2000).

Within this context the *first research question* of this thesis was formulated, i.e. does small mammal diversity of the Tagliamento river islands vary just according to measures of size and isolation or are there also other factors which can be fundamental in determining the patterns of richness, diversity and abundance of small mammals on river islands? (Research question N.1, addressed in chapter 3).

1.5 What is a landscape?

Several definitions of landscape have been proposed in the ecological literature since the emerging and recognition of landscape ecology as a discipline (e.g. Troll 1939; Turner 1989). All of them describe landscape *as a spatially heterogeneous area* and identify three characteristics describing landscapes through a dynamic and functional approach:

-*Structure*, which refers to the spatial relationships between distinctive ecosystems in the landscape, i.e., the distribution of energy, materials and species in relation to the sizes, shapes, numbers, kinds and configurations of components;

-*Function*, which refers to the interactions between the spatial elements, i.e. the flow of energy, materials and organisms among the component ecosystems;

-*Change*, which refers to alteration in the structure and function of the landscape through time.

The *structural components* of the landscape, as identified by Forman and Gordon (1981) are:

-*Patches*: Surface areas differing from their surroundings. They are physical spaces which constitute the basic units of the landscape. Patches can change and fluctuate and can serve as conduit for the movement of species, as filter inhibiting the movement of some species and facilitating that of others, as sources of species for the colonisation of other patches and as sinks (Vogiatzakis and Griffiths 2008). River islands, as the unit of habitat investigated in this thesis, can be considered as landscape patches.

-*Matrix*: background ecological system. It is represented by the kind of vegetation cover/land use which is predominant in a landscape and has a high degree of connectivity. In the context of the Tagliamento's riverine landscape, the matrix may be considered to be the gravel bars that form the active tract of the subject reach.

-*Corridors*: roughly linear strips of habitat connecting otherwise isolated patches in a functioning ecological network allowing for the dispersal of plants and animals.

The *functional characteristic*s of landscapes describe the dynamics and persistence of species among these structural components (Turner 1989). Wiens (2002) recognizes four important factors regulating these dynamics:

-*Patch quality* describes the value of the patch as habitat to the species of concern;

-*Edge effect* describes the extent to which the boundary between the patch and its surroundings influences movement of individuals within and between-patches (Forman and Godron 1981);

-*Patch context* describes the spatial location of a patch in relation to its surroundings and to other similar patches;

-*Connectivity* is a measure of the ease of movement of individuals between habitat patches within the landscape.

1.6 Rivers as landscapes

Wiens (2002) discussed three ways in which rivers and streams have been considered by landscape ecologists:

-Rivers *as linear elements of the landscape* equivalent to fields, forests, urban centres, etc.;

-Rivers *as functional parts of the landscapes* connected by boundary flows (exchanges of materials, organisms, energy) to other adjacent landscape elements;

-Rivers *as landscapes* i.e. rivers as heterogeneous entities.

The latter view of rivers derives from recognizing in them all the characteristics used above to describe landscapes (i.e. *Structure*, *Function*, *Change*) and all the factors regulating the dynamics occurring between their structural elements (*patch quality*, *edge effect*, *patch context* and *connectivity*). This is the view considered in the present thesis, where a section of the River Tagliamento will be treated as a natural landscape in which to investigate principles regulating distribution, population. community and spatial dynamics of different species of small mammals.

The *structure* of a riparian landscape describes the complex spatial array of elements constituting river landscapes and it is usually referred to as riparian mosaic (Forman 1995) (Figure 1.2). It is represented by geomorphic features (i.e. water channels, gravel bars, shorelines, etc.), which function as habitat for some species (Francis 2006; Indermaur et al. 2009; Rust 1998) and by a diversity of aquatic and riparian habitats encompassing a wide array of successional stages (i.e. ponds, riffles, shorelines, vegetated islands, riparian forest, etc.).

Figure 1.2 Distribution of vegetated islands (i.e.riparian habitats) and surface water (geomorphic features) constituting the landscape of the active riparian corridor of the River Tagliamento, NE Italy. At low and mean water levels most vegetate islands are surrounded by alluvial gravel, not water. SOURCE: Ward and Tockner 2001.

The *functional component* of riparian landscapes can be visualized through the multidimensional environmental gradients encompassing their longitudinal, lateral and vertical dimensions (Ward and Tockner 2001; Wiens 2002). Given this multiplicity of gradients, riverine landscapes have several exchange pathways for energy, materials and organisms. For example, upstream-downstream changes, especially for rivers which traverse extensive altitudinal gradients, contribute to high structural diversity and therefore enhanced biodiversity gradients (Wiens 2002). Gradients extend also laterally across the corridor, from upland through the river channel to upland on the opposite side, interrupted by distinct patches of landforms, bars pools and vegetation with different adaptations to hydrological disturbance (Figures 1.3).

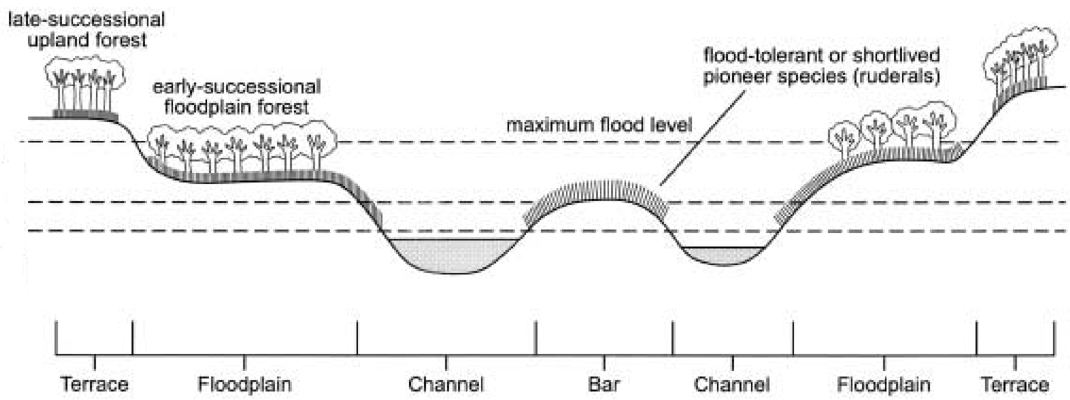


Figure 1.3 Lateral profile of a riparian corridor, displaying varying elements constituting the river mosaic and the vegetation types adapted to different levels of hydrological disturbance. SOURCE: Francis (2009).

Furthermore, in most areas the alluvial gravel matrix is highly patchy due to the presence of exposed riverine sediments, vegetated islands, abandoned channels etc.; significant lateral biotic and abiotic flows occur from the riparian forest, to the patchy alluvial matrix. The width and the composition of the riparian forest for example, can influence such things as the amount of shading that streams receives, the transfer rates of nutrients, the amount of coarse woody debris in the floodplain, rate of predation by terrestrial predators on aquatic organisms, etc. (Nakano and Murakami 2001).

Riverine landscapes are *changing* landscapes, the spatial heterogeneity of which is maintained by dynamic factors operating at different time scales (Tockner et al. 2003). For example, riverine landscapes are frequently disturbed by floods and flows of mineral and organic matter, creating a complex shifting mosaic of landforms over a large spatial and temporal scale. Floods can destroy older patches and create new ones resulting in an annual redistribution and sorting of sediment sizes and new channel configurations.

1.7 Life histories of oceanic and continental island vertebrates

On oceanic and continental islands different levels of predation, competition and resources abundance have been hypothesised to affect life history traits of vertebrates resulting in particular characteristics of island vertebrates that are collectively encapsulated in the “Island rule” and “Island syndrome”. In the next sessions these modifications and the ecological mechanisms describing them will be explained in detail.

1.7.1 The island rule and the island syndrome

Foster (1964) studied 116 island species and compared them to their mainland varieties. He documented insular size trends in six mammal groups and concluded that insular rodents tend to increase in size and artiodactyls, carnivores, and lagomorphs tend to decrease in size, with marsupials and insectivores showing no consistent trends. Later, Heaney (1978) and subsequently Lomolino (1985) reinterpreted the rule to be a graded trend from gigantism in the smaller species to dwarfism in the larger species of mammals. This phenomenon became one of the so-called eco-geographical rules; the '*island rule'*. Evidence for the existence of the island rule was proved for vertebrates (Lomolino 2005). The most recent examples include different taxa: rodents (reviewed by Adler and Levins 1994), amphibians (Montesinos et al. 2012), birds (Boyer and Jetz 2010; Potvin 2013; Scott et al. 2003), reptiles (Keehn et al. 2013; Pafilis et al. 2009; Senczuk et al. 2014), sloths (Anderson and Handley 2002) and elephants (Palombo 2007).

The variety of explanatory hypotheses for the island rule has been difficult to disentangle. Explanations focused on three primary ecological processes that differ between mainland and island environments: predation, competition, and resource availability (Palkovacs 2003). In the next three sections these three processes are presented together with some hypotheses on their consequences for the size of animals inhabiting islands. However, it should be noted that several of these hypotheses are interlinked, as suggested from the empirical evidence.

Beyond the documented differences in body size, there are several other patterns that have become apparent in insular vertebrates. These include a tendency to manifest demographic and behavioural differences in comparison to mainland populations.

Demographic differences involve divergences in density, reproductive output and age structure (e.g. Adler and Tamarin 1984). Behavioural differences are represented by an increased tolerance for conspecifics due to a more sedentary life style of insular populations (e.g. Gliwicz 1980). Adler and Levins (1994) reviewed these differences and termed them collectively, the '*island syndrome*'. Demographic and behavioural traits involved in the manifesting of the island syndrome and the underlying ecological processes are presented in detail in chapter 4, section 4.1.

The investigation of whether the populations of small mammals inhabiting the islands of the River Tagliamento manifest changes in their life history traits according to the expectations of the island syndrome and of the island rule makes the core of the *second research question* of this study and will be addressed in chapter 4.

Evidence exists that animals inhabiting oceanic islands also show differences in their spatial behaviour in respect to their mainland counterparts with island individuals showing smaller home range sizes (e.g. Sale and Arnould 2009). For some authors, these differences fall inside the concept of the island syndrome (e.g. Adler and Levins 1994; Navajas y Navarro et al. 1989) and this view will be also considered in this thesis. Spatial behaviour of island animals as compared to mainland animals and the underlying ecological process explaining such differences are presented in chapter 5, section 5.1.

The observed differences in the spatial behaviour of island animals in respect to their mainland counterparts has led the formulation of the *third research question* of this thesis, i.e. do small mammals inhabiting the river islands of the Tagliamento manifest changes in their spatial behaviour in line with what is predicted by the island syndrome? This research question will be addressed in chapter 5.

1.7.2 Predator release on islands

The hypothesis relating island rule to predator pressure, is based on the assumption that predator avoidance strategies exert significant selective pressure on body size evolution of animals on the mainland (Meiri 2008; Sundell and Norrdahl 2002). Increased body size will be favoured if an animal's predator avoidance mechanism is running away or fighting. Conversely, in smaller animals, decreased size may confer a significant advantage, because smaller species tend to adopt a 'hiding' defence strategy and commonly escape by retreating into refuges too small for predators to follow. There is empirical evidence for size-specific predation and prey size refugia, particularly in fish, amphibians, and invertebrates (Chase 1999), but such mechanisms may be less important for populations of mammals and birds, which tend to show big variation in resource use (e.g. refuges) among different age classes rather than intraspecific size variation (Werner and Gilliam 1984).

Force of predation on islands has shown to be less intense than on the mainland due to incomplete colonisation of islands by predators and because prey abundance and space are more limited (Adler and Levins 1994; Foster 1964; Lomolino 2005). If small mammals escape predation by hiding, favouring small body size, and large mammals escape predation by running or fighting, favouring large body size, then release from predation will result in a general increase in size for small mammals and a general decrease for large mammals on islands (Heaney 1978; Lawlor 1982).

Evidence of a correlation between the island rule and a reduced predator pressure on islands was found by Michaux et al. (2002) for individuals of the wood mouse (*Apodemus sylvaticus)* captured from insular and mainland populations of Western Europe. Investigated islands (e.g. Sardinia, Sicily, Mallorca, Port Cros, Marettimo) differing in size (range 6.5-25711km^2) where characterized by lower number of predators than the mainland areas (in Iberian peninsula and Italy) and in general by increased size of *A. sylvaticus* individuals.

1.7.3 Competitive release/niche expansion on islands

Given that species richness is higher on the mainland than on the islands and that it declines with the decreasing of island size (MacArthur and Wilson 1967), islands should have fewer competitor species relative to the mainland and large islands should have more competitor species than small islands. Therefore extant fauna on (small) islands may be enabled to expand their ecological niche and therefore to occupy habitat and utilise food resources which would otherwise be unavailable to them, a process called *competitive release* (Grant 1972).

If larger individuals, in absence of competitors, have greater niche breadths since they can, for instance, eat large as well as small food items, selection would favour an overall increase in size on islands (Diamond 1970; Roughgarden 1972; Valen 1965). Supporting this view, Heaney (1978) observed a decrease in body size of Southeast Asian tri-coloured squirrels on large islands relative to medium sized islands, as a consequence of increasing importance of interspecific competition on larger islands (i.e. greater diversity and abundance of interspecific competitors). More recently, niche expansion leading to increased body size has been studied in the house mouse (*Mus musculus*) of Gough Island, South Atlantic. The mice introduced to Gough Island in 1810 have evolved to eat exclusively Tristan Albatross (*Diomedea dabbenena*) chicks and grow to twice the size of a normal house mouse on average as a result (Wanless et al. 2007).

According to Adler and Levins (1994) there is another explanation as to how an increase in body size is related to competition mechanisms on islands, which is based on the increased availability of food resources in conditions of competitor release. An increase in available resources is likely to result in increased densities, particularly if the influence of predation is negligible and dispersal is limited (see section 4.1, chapter 4). As a consequence of increased densities, increased intraspecific competition may also occur, which in turn may select for increased body size in the long-term (Adler and Levins 1994). A few recent examples clarify and explain some of the mechanisms which have been studied in relation to insular gigantism (i.e. decreased interspecific competition and increased intraspecific competition).

Wu et al. (2006) have found significant increases in body size of rice frogs (*Rana limnocharis*) in the Zhoushan Archipelago, China. They explained that increased resource availability on islands has led to higher carrying capacities, which subsequently has facilitated higher densities and individual growth rates, resulting in larger body size in rice frogs. They also suggest that large body size evolved on islands because larger individuals are competitively superior under conditions of harsh intraspecific competition at high densities.

Another more recent example of how inter- and intraspecific competition drives body size evolution is represented by wall lizards (*Podarcis gaigeae*) (Pafilis et al. 2009) on Skyros island and its satellite islets (Aegean Sea). This species exhibits island gigantism on small islets surrounding Skyros. Islets are characterized by fewer predators (snakes mainly) and competitors in respect to Skyros but show higher numbers of nesting seabirds. Seabirds subsidize islands ecosystems by importing nutrients in the form of guano, fish scraps, and carcasses therefore supporting dense lizard populations. The authors found that on islets, in conditions of higher resource availability (i.e. more seabirds means more luxurious and more nitrophilous vegetation and higher arthropod densities), densities of lizards were higher, intraspecific competition (quantified through rates of cannibalism and field autotomy) stronger and body size of lizards larger. In predator-free islands, lizards occur in higher densities and juveniles tend to evolve large size to escape predation and intraspecific competition (Pafilis et al. 2009).

1.7.4 Resource availability on islands

The survival of individuals in a given population is obviously intrinsically linked to food resource availability in that without adequate food supplies, individuals and possibly populations will not persist. In the previous section it is explained how in small animals, increased resource availability on islands (as a consequence of reduced interspecific competition), would result in increased densities and therefore in increased intraspecific competition which would select for increased body size. According to the ‘area scaling hypothesis’ (Marquet and Taper 1998), while increased intraspecific competition could theoretically select for increased body size in small animals, there is a constraint on species of large size: body size affects the number of animals that can live in a given area. Furthermore, one of the most relevant disadvantages of having a large size is an increase in total energy and resource requirements, which would be especially problematic on small islands and on those ones with few predators, but high population densities and intense intraspecific competition. On the contrary, in the absence of predators, the energy used to outgrow, outrun or outfly them on the mainland could be used to adapt more efficiently to insular environments and their ecologically simple communities, permitting a larger population to be maintained, which in turn increases the probability of population survival (Lomolino 2005).

Providing some examples about these mechanisms McNab (1994a, b), discussed which factors reduce rate of energy expenditure in rails on oceanic islands, which evolved a decrease in body mass and flightlessness. The author discussed that abundance of birds in general is regulated by the abundance of food and other resources, and by the presence of competitors and predators. Most oceanic islands where rails occur, are depauparate in competitors and completely lack mammalian predators. The absence of mammalian predators is central to the evolution of flightlessness in birds, according to McNab (1994a). In the absence of mammalian predation, birds may increase their use of resources in an environment up to a limit represented by resource abundance. When populations are resource limited, a reduction in individual energy expenditure may result from intraspecific competition. A reduction in individual food intake would lead to a reduction in individual home range size, in part because home range in birds is correlated with body mass (Schoener 1968). Consequently, using the same resources, small flightless rails would likely maintain larger populations on small islands than large flighted rails.

1.8 Life histories traits of habitat island vertebrates

Predator release, competitor release, enlargement of the ecological niche and differences in resource availability have been described in the previous sections as being responsible for changes in evolutionary and life history traits in oceanic and continental islands. It is important to consider these in relation to habitat islands, which differ from oceanic islands, as noted above.

Evidence suggests that populations of vertebrates inhabiting isolated habitat islands may show adaptive responses to their changed conditions, displayed in body size and life history characteristics (e.g. Lomolino and Perault 2007 for *small mammals*; Vargas et al. 2012 for *birds*; Wang 2009 for *reptiles*). The mechanisms responsible for driving these changes on oceanic islands have been investigated to an extent in habitat islands, for example:

Predator release has not been formally investigated in relation to its effect on the body size of prey species in fragmented landscapes. Other effects have been highlighted, however. For example, Crooks and Soulè (1999) studied spatial and temporal variation in the distribution and abundance of an apex predator, the coyote

(*Canis latrans*), in a landscape fragmented by agricultural development. They found that the decline and disappearance of the coyote, in conjunction with the effects of habitat fragmentation, affected the distribution and abundance of smaller carnivores and the persistence of their avian prey. Moreover, it has been shown that in fragmented landscapes rates of predation on small mammals are higher at or near edges than at interior sites of habitat islands (Sàlek et al. 2010; Wolf and Batzli 2004). A portion of this increased predation has been attributed to a numeric response by predators to the greater density of prey that is often associated with habitat edges (Salek et al. 2010; Schmidt and Whelan 1999).

In studies examining the responses of *single species* to habitat fragmentation it has been shown that body size can change as an effect of *changes in resource availability* in smaller habitat patches as compared to larger ones. Barbour and Litvaitis (1999) examined physical condition and niche dimensions of New England cottontails (*Sylvilagus transitionalis*) that occupied 21 woodland patches of different sizes in New England (USA) during winter. Rabbits on small patches (<2.5 ha) were predominantly males, and both sexes had lower body mass than individuals on large patches (>5.0 ha). Niche indices of habitat use revealed that rabbits on small patches used a greater variety of microhabitats than rabbits occupying large patches. Rabbits on small patches also consumed low quality forage more often and fed at sites farther from escape cover than rabbits on large patches. *Niche expansion* was not a result of competitor release. Rabbits on small patches apparently modified their niche dimensions in response to resource limitations. This response included occupying sites with limited understory cover that apparently resulted in rabbits in small patches having a lower survival rate than rabbits in large patches during a 10-week monitoring period.

At *community level*, studies investigating the effect of habitat fragmentation on small mammal communities represented by several competitor species, have shown how habitat specialists and habitat generalists may respond differently to the changed conditions of habitat due to fragmentation. Habitat generalists are usually more adaptable and can even increase their abundances in small isolated habitat patches (Diaz et al. 1999; Mortelliti et al. 2009), whereas habitat specialists besides being affected by a reduction in the size of a habitat patch (Mortelliti et al. 2009) are in general more sensitive to the quality and abundance of food and cover resources in that patch (Marsh and Harris 2000). Therefore the relative distribution and abundance of competitor species in a fragmented landscape can reflect a spatial segregation of habitat generalists and specialists according to habitat quality, cover and connectivity (Marsh and Harris 2000). If the segregation is partial, different competitor species in the same habitat patch may affect the survival and reproduction of local species populations (Sozio and Mortelliti 2015).

Based on this evidence, it may therefore be reasoned that if differences are observed in species diversity, life history and spatial behaviour between insular and mainland populations of selected small mammals along the River Tagliamento, conditions of predator release, competitor release, enlargement of the ecological niche and resource availability are the likely mechanisms underpinning this. This then raises the question of which of them operate on the river islands of the Tagliamento, and which are the most important. Therefore, within the context of the three main research questions of this thesis, it will be investigated and discussed whether any detected differences in species diversity, life histories and spatial behaviour of river island small mammals depend upon variation in resource availability and relative densities of competitors between the riparian forest and the islands or by intrinsic differences in life histories of different species. Specific predictions about each research question are reported in the following sections.

1.9 Thesis structure and aims

The research was conducted in the riparian part of the wider river mosaic of the river, i.e. the sections of the mosaic subjected to periodic inundation but being mainly terrestrial (gravel bars, islands, riparian forest). The riparian forest will represent the ‘mainland habitat’ or the ‘continuous habitat’, while the river islands will represent the ‘patchy habitat’.

This thesis consists of 7 chapters, the present included. Chapter 2 is devoted to the description of the study area, of the data sampling protocol and to a listing and a description of the species recorded during the fieldwork on the Tagliamento. Chapters 3, 4 and 5 represent the main core of the thesis and are devoted to addressing the research questions presented in the previous sections of this chapter. Chapter 6 provides an exploratory analysis on the use carnivore species make of the Tagliamento river islands to gain an insight on the potential predator pressure small mammal experience in the riparian mosaic of the Tagliamento. Chapter 7 reports the general discussion and the conclusions.

Chapter 2

This chapter describes the study area in fine detail and presents the main results of a pilot study carried out in 2009, which informed the data collection and the sampling protocol of the data presented and analysed in this thesis. The chapter ends with a description of the major biological and ecological traits of the focal species.

Chapter 3 - Research question N. 1

The core of this chapter is represented by an analysis of the variables affecting small mammal species diversity of the river islands of the Tagliamento riparian mosaic. The theoretical framework for this chapter is represented by landscape ecology principles, according to which species diversity on habitat islands is regulated not only by their size and isolation but also by other spatial aspects of the landscape (i.e. the presence and permeability of the matrix), disturbance factors, alongside the dispersal capabilities of the species and the availability of food resources. Furthermore as observed in several landscape ecology studies and in insular biogeography, mechanisms of interspecific competition can also be important in regulating species richness and diversity on habitat islands, and are considered here.

Specific questions addressed in this chapter were: (1) which variables affect species diversity and the structure of small mammal communities on river islands differing in size, isolation, resource availability and degree of disturbance (flooding) acting on them? (2) how are all these factors interacting in determining small mammal species diversity?

The prediction was that small mammal species diversity on river islands was regulated by the size and the spatial context of islands and also by the availability of food resources for small mammals (subsidising mechanisms of interspecific competition) and by their ephemeral nature due to periodic disturbance.

Chapter 4 - Research question N. 2

In this chapter morphological and demographic parameters of island and riparian forest populations of three rodent species (*Apodemus flavicollis*, *A. sylvaticus*, *A. agrarius*) were investigated to see whether their populations conform to patterns predicted by the '*island syndrome*'. Specifically, it was explored whether there was evidence of differences between insular and riparian forest populations in the following parameters: (i) density, (ii) rodent biomass, (iii) reproductive output, (iv) age structure (v) body weight.

It was predicted that a difference in resource availability for small mammals between the riparian forest and the islands reflected a difference in the composition of the community, in the reproductive output and in the age structure of small mammal populations inhabiting the two habitats. Furthermore, given that the dynamics of animals inhabiting river islands are periodically disturbed by stochastic events like floods it was also expected that possible changes in body size would be periodically re-set, therefore being difficult to detect.

Chapter 5 - Research question N. 3

The focus of this chapter is the study of the spatial dynamics of males of *A. agrarius* on the riparian mosaic of the Tagliamento. This chapter is partly based on aspects of the island syndrome related to the spatial behaviour of insular mammals and partly on principles of landscape ecology related to the influence of the spatial configuration of resources on animal movements.

Two hypotheses concerning the existence of a different spatial behaviour between riparian forest and insular individuals were tested (1) Average home range size was hypothesized to be larger in insular individuals than in riparian forest individuals; (2) Number of core areas was hypothesized to be higher in insular individuals than in riparian forest individuals. These two hypotheses were based on the assumptions that the (1) availability of food and cover resources is lower on islands, (2) patchy displacement of food and cover resources affects home range size of small mammals on islands, (3) density of competitors is lower on islands, and (4) patchy displacement of food resources and intense edge effects characterise islands on the Tagliamento floodplain, therefore pushing animals to move more to satisfy their daily needs.

Chapter 6

In this chapter, summer and autumn distribution data (i.e. presence/absence data) of the stone marten (*Martes foina*) were analysed to explore what are the factors that might affect the use this carnivore species makes of the riparian mosaic of the Tagliamento. Logistic regression models were used to investigate the relationship between presence/absence of stone marten and (1) the spatial characteristics, and (2) the availability of food resources present on the investigated mainland and island sites. These data were collected to gain an insight on the potential predator pressure small mammals experience in the riparian mosaic of the Tagliamento. This chapter is partly based on landscape ecology, whereby predictions that stone martens should have a higher probability of presence on sites that are larger in size, less isolated and richer in food resources are made.

Chapter 7

This chapter synthesizes what has been discovered through the research presented in the thesis, and relates it to the main theories of island biogeography and landscape ecology. The key findings were then considered against those listed by Adler and Levins (1994) and Vincente (1999) as typical of oceanic island communities, to check to what degree the Tagliamento system fits the predictions made for oceanic islands and to what degree the results fit with landscape ecology studies. With this structure the discussion gives an answer to the three main research questions of thesis.

1.10 References

Adler, G.H. and Tamarin, R.H., 1984. Demography and reproduction in island and mainland white-footed mice (Peromyscus leucopus) in southern-eastern Massachusetts. Canadian Journal of Zoology 62, 58-64.

Adler, G.H. and Levins, R., 1994. The island syndrome in rodent populations. Quarterly Review of Biology 69, 473-490.

Anderson, R.P. and Handley Jr, C.O., 2002. Dwarfism in insular sloths: Biogeography, selection, and evolutionary rate. Evolution 56, 1045-1058.

Arscott, D.B., Tockner, K., Van der Nat, D., Ward, J.V., 2002. Aquatic habitat dynamics along a braided Alpine river ecosystem (Tagliamento river, Northeast Italy). Ecosystem 5, 802-814.

Barbour, M.S. and Litvaitis, J.A., 1999. Niche dimensions of New England cottontails in relation to habitat patch size. Oecologia 95, 321-327.

Bender, D.J. and Fahrig, L., 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. Ecology 86, 1023–1033.

Boyer, A.G. and Jetz, W., 2010. Biogeography of body size in Pacific Island birds. Ecography 33, 369-379.

Brown, J.H., 1971. Mammals on mountaintops: Nonequilibrium insular biogeography. American Naturalist 105, 467-478.

Brown, J.H. and Lomolino, M.V., 1998 Biogeography, Second ed, p.692.

Chase, J.M., 1999. Food web effects of prey size refugia: Variable interactions and alternative stable equilibria. American Naturalist, 154, 559-570.

Crooks, K.R. and Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400, 563-566.

Debinski, D.M and Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14, 342-355.

Diamond, J.M., 1970. Ecological consequences of island colonization by Southwest Pacific Birds, I. type of niche swifts. Proceedings of the National Academy of Sciences USA 2, 529-536.

Diaz, M., Santos, T., Telleria, J.L., 1998. Effects of forest fragmentation on the winter body condition and population parameters of an habitat generalist, the wood mouse Apodemus sylvaticus: a test of hypohtesis. Acta Oecologica 20, 39-49.

Dynesius, M. and Nilsson, C., 1994. Fragmentation and flow regulation in the northern third of the world. Science 266, 753-762.

Forman, R.T.T. and Godron, M., 1981. Patches and structural components for a landscape ecology. BioScience 31, 733-740.

Forman, R.T.T., 1995. Land mosaics. The ecology of landscapes and regions, 7 edn. Cambridge University Press.

Foster, B.L., 1964. Evolution of mammals on islands. Nature 202, 234-235.

Fox, B.J. and Fox, M.D., 2000. Factors Determining Mammal Species Richness on Habitat Islands and Isolates: Habitat Diversity, Disturbance, Species Interactions and Guild Assembly Rules. Global Ecology and Biogeography 9, 19-37.

Francis, R.A., 2006. Allogenic and autogenic influences upon riparian vegetation dynamics. Area 38, 453-464.

Francis, R.A., 2009. Ecosystem prediction and management, In A companion to Environmental Geography. ed. N.D. Castree, D., Liverman, D. and Rhoads, B. (eds), pp. 421-441. Blackwell, London.

Frey, J.K., Bogan, M.A., Yates, T.L., 2007. Mountaintop island age determines species richness of boreal mammals in the American Southwest. Ecography 30, 231-240.

Gliwicz, J., 1980. Island populations of rodents - their organization and functioning. Biological Reviews of the Cambridge Philosophical Society 55, 109-138.

Grant, P.R., 1972. Convergent and divergent character displacement. Biological Journal of the Linnean Society 4, 39-68.

Gurnell, A.M. and Petts, G.E., 2002. Island-dominated landscapes of large floodplain rivers, a European perspective. Freshwater Biology 47, 581-600.

Habersack, H.M., 2000. The river-scaling concept (RSC): a basis for ecological assessments. Hydrobiologia 422/423, 49-60.

Haila Y., 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. Ecological Applications 12, 321–334.

Heaney, L.R., 1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (Callio-sciurus prevosti) of Southwest Africa. Evolution 32, 29-44.

Indermaur, L., Gehring, M., Wehrle, W., Tockner, K., Naef-daenzer, B., 2009. Behavior-based scale definitions for determining individual space-use: requirements of two amphibians. The American Naturalist 173, 60-70.

Keehn, J.E., Nieto, N.C., Tracy, C.R., Gienger, C.M., Feldman, C.R., 2013. Evolution on a desert island: Body size divergence between the reptiles of Nevada's Anaho Island and the mainland around Pyramid Lake. Journal of Zoology 291, 269-278.

Kupfer, J.A., Malanson, G.P., Franklin, F.P., 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation. Global Ecology and Biogeography 15, 8–20.

Lake, P.S., Bond, N., Reich, P., 2007. Linking ecological theory with stream restoration. Freshwater Biology 52, 597-615.

Lawlor, T.E., 1982. The Evolution of Body Size in Mammals: Evidence from Insular Populations in Mexico. The American Naturalist 119, 54-72.

Lehmkuhl, J.F., Peffer, R.D., O'Connell, M.A., 2008. Riparian and upland small mammals on the east slope of the Cascade Range, Washington. Northwest Science 82, 94-107.

Lomolino, M., 1985. Body size of mammals on islands: The island rule reexamined. The American Naturalist 125, 310-316.

Lomolino, M.V., 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32, 1683-1699.

Lomolino, M. and Perault, D.R., 2001. Island biogeography and landscape ecology of mammals inhabiting fragmented, temperate rain forests. Global Ecology & Biogeography 10, 113-132.

Lomolino, M.V. and Perault, D.R., 2007. Body size variation of mammals in a fragmented, temperate rainforest. Conservation Biology 21, 1059-1069.

MacArthur, R.H. and Wilson, E.O., 1967. The Theory of Island biogeography. Princeton University Press.

MacArthur, R.H., Karr, J.M., Diamond, J.M., 1972: Density compensation in islands faunas. Ecology 53, 330–342.

Marquet, P. and Taper, M., 1998. On size and area: Patterns of mammalian body size extremes across landmasses. Evolutionary Ecology 12, 127-139.

Marsh, A.C.W. and Harris, S., 2000. Partitioning of woodland habitat resources by two sympatric species of Apodemus: Lessons for the conservation of the yellow-necked mouse (A. flavicollis) in Britain. Biological Conservation 92, 275-283.

Mayr, E., 1967. The challange of island faunas. Australian Natural History 15, 359-374.

McNab, B.K., 1994a. Energy conservations and the evolution of flightlessness in birds. Amercan Naturalist 144, 628-642.

McNab, B.K., 1994b. Resource Use and the Survival of Land and Freshwater Vertebrates on Oceanic Islands. The American Naturalist 144, 643-660.

Meier, K., Kuusemets, V., Luig, J., Mander, U., 2005. Riparian buffer zones as elements of ecological networks: Case study on Parnassius mnemosyne distribution in Estonia. Ecological Engineering 24, 531-537.

Meiri, S., 2008. Evolution and ecology of lizard body sizes. Global Ecology and Biogeography 17, 724-734.

Mendenhall, C.D., Karp, D.S., Meyer, C.F.J., Hadly, E.A., Daily, G.C., 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. Nature 509, 213-217.

Michaux, J.R., De Bellocq, J.G., Sara, M., Morand, S., 2002. Body size increase in insular rodents populations: a role for predators? Global Ecology & Biogeography 11, 427-436.

Montesinos, R., da Silva, H.R., de Carvalho, A.L.G., 2012. The 'Island Rule' Acting on Anuran Populations (Bufonidae: Rhinella ornata) of the Southern Hemisphere. Biotropica 44, 506-511.

Mortelliti, A., Amori, G., Annesi, F., Boitani, L., 2009. Testing for the relative contribution of patch neighborhood, patch internal structure, and presence of predators and competitor species in determining distribution patterns of rodents in a fragmented landscape. Canadian Journal of Zoology 87, 662-670.

Naiman, R.J., Decamps, H., Pollock, M.M., 1993. The role of riparian corridors in mantaining regional biodiversity. Ecological Applications 3, 209-212.

Nakano, S. and Murakami, M., 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences USA 98, 166-170.

Navajas y Navarro, M., Cassaing, J., Croset, H., 1989. Demographie et dispersion d'une population sauvage insulaire de Mus musculus domesticus: comparison avec une population continentale. Z. Saeugetierkd. 54, 286-295.

Pafilis, P., Meiri, S., Foufopoulos, J., Valakos, E., 2009. Intraspecific competition and high food availability are associated with insular gigantism in a lizard. Naturwissenschaften 96, 1107-1113.

Palombo, M.R., 2007. How can endemic proboscideans help us understand the "island rule"? A case study of Mediterranean islands. Quaternary International 169-170, 105-124.

Palkovacs, E.P., 2003. Explaining adaptive shifts in body size on islands: a life history approach. Oikos 103, 37-44.

Petts, G.E., Moller, H., Roux, A.L., (eds.), 1989. Historical changes of Large Alluvial Rivers, Western Europe. Wiley, Chichester, UK.

Pires, A.S., Koeler Lira, P., Fernandez, F.A.S., Schittini, G.M., Oliveira, L.C., 2002. Frequency of movements of small mammals among Atlantic Coastal Forest fragments in Brazil. Biological Conservation 108, 229-237.

Potvin, D.A., 2013. Larger body size on islands affects silvereye Zosterops lateralis song and call frequency. Journal of Avian Biology 44, 221-225.

Prevedello, J.A., Forero-Medina, G., Vieira, M.V., 2010. Movement behaviour within and beyond perceptual ranges in three small mammals: effects of matrix type and body mass. Journal of Animal Ecology 79, 1315-1323.

Ricketts T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. American Naturalist 158, 87–99.

Robichaud, I., Villard, M.A., Machtans, C.S., 2002. Effects of forest regeneration on songbird movements in a managed forest landscape of Alberta, Canada. Landscape Ecology 17, 247-262.

Roughgarden, J., 1972. Evolution of Niche Width. The American Naturalist 106, 683-718.

Rust, C., 1998. Die okologische Bedeutung von Inseln und Schotterbanken im Tagliamento (Friaul, Italien) am Beispiel der Laufkaferzonose (Carabidae, Insecta). Diplomarbeit, ETH Zurich.

Sale, M.G. and Arnould, J.P.Y., 2009. Spatial and temporal organization in the swamp antechinus: comparison between island and mainland populations. Journal of Mammalogy 90, 347-355.

Šálek, M., Kreisinger, J., Sedláček, F., Albrecht, T., 2010. Do prey densities determine preferences of mammalian predators for habitat edges in an agricultural landscape? Landscape and Urban Planning 98, 86-91.

Sanchez, B.C., andParmenter, R.R., 2002. Patterns of shrub-dwelling arthropod diversity across a desert shrubland-grassland ecotone: A test of island biogeographic theory. Journal of Arid Environments 50, 247-265.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5, 18-32.

Schmidt, K.A. and Whelan, C.J., 1999. Nest predation on woodland songbirds: When is nest predation density dependent? Oikos 87, 65-74.

Schoener, T., 1968. Sizes of feeding territories among birds. Ecology 49, 123-141.

Scott, S.N., Clegg, S.M., Blomberg, S.P., Kikkawa, J., Owens, I.P.F., 2003. Morphological shifts in island-dwelling birds: The roles of generalist foraging and niche expansion. Evolution 57, 2147-2156.

Senczuk, G., García, A., Colangelo, P., Annesi, F., Castiglia, R., 2014. Morphometric and genetic divergence in island and mainland populations of Anolis nebulosus (Squamata: Polychrotidae) from Jalisco (Mexico): An instance of insular gigantism. Italian Journal of Zoology 81, 204-214.

Shirley, S.M., 2006. Movement of forest birds across river and clearcut edges of varying riparian buffer strip widths. Forest Ecology and Management 223, 190-199.

Sozio, G. and Mortelliti, A., 2015. Empirical evaluation of the strength of interspecific competition in shaping small mammal communities in fragmented landscapes. Landscape Ecology, 15 p. Article in Press.

Sundell, J. and Norrdahl, K., 2002. Body size-dependent refuges in voles: an alternative explanation of the Chitty effect. Annales Zoologici Fennici 39, 325-333.

Tockner, K., Ward, J.V., Arscott, D.B., Edwards, P.J., Kollmann, J., Gurnell, A.M., Petts, G.E., Maiolini, B., 2003. The Tagliamento river: a model ecosystem of European importance. Aquatic Science 65, 239-253.

Troll, C. 1939. Luftbildplan und Ökologische Bodenforschung. Z.Ges. Erdkunde, 241–298.
Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Ann. Rev. Ecol. Syst. 20, 171-197.

Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Ann. Rev. Ecol. Syst. 20, 171-197.

Turner, F.J., 1998. Landscape ecology, living in a mosaic., In Ecology. eds S.I. Dodson, T.F. Allen, S.R. Carpenter, A.R. Ives, R.J. Jeanne, J.F. Kitchell, N.E. Langston, M.G. Turner, pp. 78-122. Oxford University Press, New York.

Valen, L.V., 1965. Morphological Variation and Width of Ecological Niche. The American Naturalist 99, 377-390.

Vandermeer, J. and Carvajal, R., 2001. Metapopulation dynamics and the quality of the matrix. American Naturalist, 158, 211-220.

Vargas, R.R., Fontúrbel, F.E., Bonacorso, E., Simonetti, J.A., 2012. Variation in reproductive life-history traits of birds in fragmented habitats: A review and meta-analysis. Bird Conservation International 22, 462-467.

Vicente, L., 1999. Evolutionary strategies in insular environments. Natura Croatica 8, 301-323.

Vogiatzakis, I. and Griffiths, G., 2008. Island Biogeography and Landscape Ecology, In Mediterranean Island Landscapes. eds I. Vogiatzakis, G. Pungetti, A.M. Mannion, pp. 61-81. Springer Netherlands.

Wanless, R.M., Angel, A., Cuthbert, R.J., Hilton, G.M., Ryan, P.G., 2007. Can predation by invasive mice drive seabird extinctions? Biology letters 3, 241-244.

Ward, J.V., Tockner, K., Edwards, P.J., Kollmann, J., Bretschko, G., Gurnell, A.M., Petts, G.E., Rossaro, B., 1999. A reference river system for the Alps: The fiume Tagliamento. River Research and Applications 15, 63-75.

Ward, J.V. and Tockner, K., 2001. Biodiversity: Towards a unifying theme for river ecology. Freshwater Biology 46, 807-819.

Werner, E.E. and Gilliam, J.F., 1984. The Ontogenetic Niche and Species Interactions in Size-Structured Populations. Annual Review of Ecology and Systematics 15, 393-425.

Whittaker, R.J. (eds.) (1998) Island Biogeography: ecology, evolution and conservation. Oxford University Press, Oxford. pp. 285.

Wiens, J.A., 2002. Riverine landscapes: taking landscape ecology into the water. Freshwater Biology 47, 501-515.

Wolf, M. and Batzli, G., 2004. Forest edge - High or low quality habitat for white-footed mice (Peromyscus leucopus)? Ecology 85, 756-769.

Wu, Z., Li, Y., Murray, B.R., 2006. Insular shifts in body size of rice frogs in the Zhoushan Archipelago, China. Journal of Animal Ecology 75, 1071-1080.

Chapter 2 - Overview of the River Tagliamento study system, mammal diversity and sampling protocols

2.1 Study system

The fieldwork that forms the basis for this thesis took place in the floodplain of the River Tagliamento in the eastern Alps in Italy (Figure 2.1). The river Tagliamento is characterized by an expansive braided floodplain with an unconstrained gravel-bed and retains the dynamic nature and morphological complexity that must have been typical of most Alpine rivers in their pristine conditions (Ward et al. 1999). This river is indeed considered to be the last morphologically intact river in the Alps and has been the focus for many studies focusing on aquatic and riparian ecology (e.g. Lippert et al. 1995; Tockner et al. 2003; Ward et al. 1999). The catchment area extends over 2580km^2. From its headwaters, in the limestone North- eastern Alps at an altitude of 1195 a.s.l., to its mouth, in the Adriatic Sea, the Tagliamento has a course of 172km (Figure 2.1). The Tagliamento floodplain is composed of two major habitat types, the active tract and the fringing riparian forest.

2.1.1 The active tract of the Tagliamento

Exposed gravel sediments, water channels and vegetated islands, dominate the active tract. Within this tract, uprooted trees are often deposited on gravel bars during floods (Gurnell et al. 2001). These trees trap sediment, wood and seeds, enlarging laterally and vertically to form *pioneer islands*. These in turn enlarge and coalesce to form *building islands* and eventually develop into large *established islands* (Figure 2.2) in a process that lasts at least seven years (Gurnell et al. 2001).

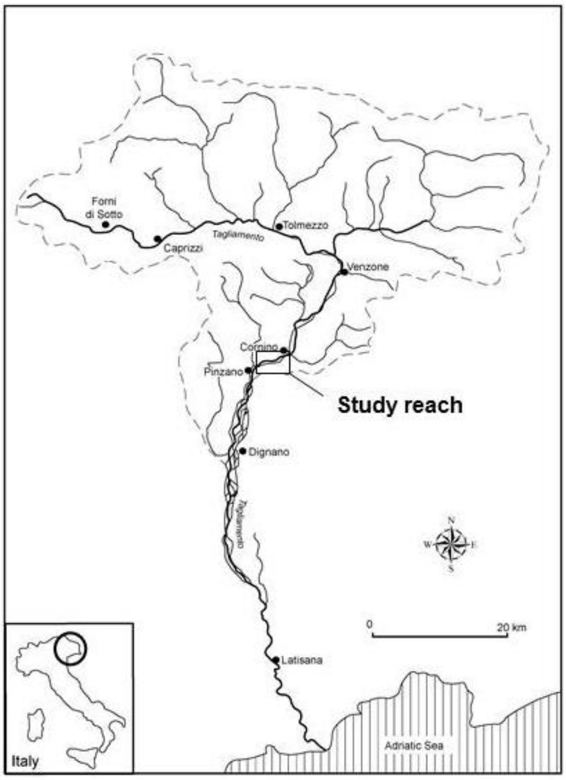


Figure 2.1 Catchment of the River Tagliamento with major tributaries and towns. The onset shows the location of the catchment within Italy (modified after Francis et al. 2008). The small rectangle identifies the section of the river where this study took place.

An island is classified as established when more than 75% of the ground surface is covered by trees, shrubs and herbaceous vegetation, with a minimum spatial extent of three canopy trees. In the study site, pioneer islands have a mean area of 44m^2±8.6 and are between two and five years old while established islands have a mean area of 0.87ha±0.9 and are between seven and 40 years old (Kollman et al. 1999; Mardhiah et al. 2015). Building islands are variable and present conditions somewhere in between these two stages.

Figure 2.2 Example of two established islands in the study area. Photo: F. Iordan, summer 2011.

The ephemeral nature of islands in the active tract

The active tract is characterized by constant repositioning of the islands due to cycles of island formation and destruction driven by catchment hydrology and vegetation regeneration. Flooding events along the study site (Figure 2.3) occur on a yearly basis but with varying intensity. The frequency and magnitude of the floods in relation to the rate of vegetation establishment and island growth is critical to island survival (Gurnell et al. 2001).

The process of island formation and destruction has been investigated in the study area by different authors. Kollman et al. (1999) mapped landscape changes by comparing aerial photographs across two time periods (1984-1986 and 1986-1991). They showed that, although the total area covered by islands had remained approximately the same, there was only a small overlap between islands that were present in 1984 and those present in 1991. This illustrates the ephemeral nature of islands and the rapid rate at which riparian trees can establish on areas of open gravel (Francis 2007).

Figure 2.3 The Tagliamento floodplain in conditions of high flood. Islands appear completely surrounded by water. The picture was taken on the 1st of November 2010 through an automatic camera positioned on the Monte of Ragogna, in front of the study area.

Kollmann et al. (1999) concluded that succession from open gravel to established islands takes between 10 and 20 years. Once formed islands can then persist for decades, but their median age is 10 years (Karrenberg et al. 2003). Zanoni et al. (2008), by analyzing historical aerial images of the study area from 1944 to 2005, came to the conclusion that established islands rarely persist for more than 24 years. There are exceptions however, as Mardhiah et al. (2015) recently demonstrated (Figure 2.4). Their study used dendrochronology and oblique photographs and showed that there are some established islands that are at least 40 years old (e.g. I6 in Table 2.1).

Figure 2.4 Photographs of a section of the study site taken during the summer in 1999, 2001, 2005, 2008, 2010 and 2012. The pictures were extracted from the study of Mardhiah et al. (2015) with the permission of the authors.

The age and height of the islands are important as they determine the probability of islands being washed away by floods (Kollman et al. 1999). Sediment deposition increases with age making islands higher in elevation: 0.3-0.8m for pioneer islands; 1.0-1.5m for building islands; and ~ 2m for established islands (Gurnell and Petts 2006).

The system is clearly *ephemeral* but the time scale across which these changes take place is greater than the time scale of the present study, which spans two years (2009-2011). In this study, only established islands were investigated and the 19 chosen islands remained relatively stable across the sampling period between December 2008 and January 2011. However, it is important to be aware of the ephemeral nature of the islands, as this is a factor that may influence the population of small mammals in this habitat.

Vegetation composition of islands

The islands are covered by riparian woodland dominated by poplar (*Populus alba and P. nigra*), willow (*Salix spp.*) and alder (*Alnus incana*) (Edwards et al. 1999; Francis et al. 2008; Kollmann et al. 1999; Tockner et al. 2003).

Pioneer islands are characterized by a dense canopy of woody vegetation up to four meters high, comprised mainly of poplar and willow (Kollman et al. 1999). A shrub layer of *P. nigra* and *Salix spp*. is usually well developed and the ground layer is correspondingly sparse and composed by a species-rich community of herbs and grasses. Established islands are occupied mostly by *P. nigra* and *A. incana* trees (up to 20m high). Shrub cover is quite sparse and composed of various species of willow (especially *S. alba*, *S. eleagnos* and *S. purpurea*) and also by *Cornus sanguinea*, *Corylus avellana*, *Crataegus spp*. and *Amorpha fruticosa.* Ground cover is dense and represented by *Rubus coesius*, herbs and grasses. Kollmann et al. (1999) also showed that the number of plant species was positively related to island area and was sustained across the developmental sequence of island types (deposited tree → pioneer island→ building island → established island).

2.1.2 The riparian forest of the Tagliamento

The total extent of the riparian forest fringing the Tagliamento active tract covers approximately a surface of $32km^2$. The sections of the forest which are not disturbed by floods are dominated by oak (*Quercus spp.)* poplars and alder with a dense understory represented by *C.avellana*, *C. sanguinea*, *Fraxinus spp.* and *Crataegus spp*. (Figure 2.5). Other common tree species are *Ulmus spp.* and *Acer spp*.

Figure 2.5 Riparian forest at the study site. One of the internal water channels is visible at the centre of the picture on the left. Photo: F. Iordan.

To be consistent with the island biogeography approach, in this thesis the term "Mainland" will be used to indicate the riparian forest, this being considered the habitat which acts as source for the animals inhabiting or visiting the active tract and the islands.

2.2 Description of the study area and selected sites

The river section chosen for this study is located within a nature reserve, with little human interference. The study area was four kilometers long and included the riparian forest (mainland) on the right bank of the river and the adjacent floodplain, including 19 islands (Figures 2.6 and 2.7). It was located 78km from the source of the river at an altitude of 135m a.s.l. The maximum width of the floodplain at the site was 800m. The floodplain comprised a complex mosaic of vegetated islands, a braided network of main and secondary channels, backwaters and ponds, all embedded within a matrix of exposed river sediments.

The left bank, which was outside the study area, hosted the hill-sloped forest of Monte Ragogna. Along the right bank, the riparian forest extends inland to a distance of 0.5-1km.

The study area was chosen because of relatively high habitat heterogeneity and because previous studies indicated that local mammal diversity was high at the site and in the surrounding areas, increasing the potential for data collection (Katulic 2003; Lapini 2009). The choice of the area was guided also by logistic issues as it was important to be able to check all the live-capture mammal traps within about five hours to release the trapped animals within a reasonable time. The chosen area was suitable because it hosted a sufficient number of established islands differing in size and distance from the mainland to test some of the research questions introduced in chapter 1, section 1.9. Only established islands were selected because, being at least seven years old, these were more likely to host populations of small mammals. Adjacent vegetated patches were considered as separate islands if the exposed gravel and/or water area between them was continuous, clearly defined and with a width greater than 10m (Zanoni et al. 2008).

A total of six large (area ≥ 1ha), eight medium (0.1ha < area < 1ha) and five small (area ≤ 0.1ha) islands were studied (Table 2.1 and Figure 2.7). Islands were classified into small/medium and large on the basis of being respectively smaller/approximately similar or larger than individual home ranges measured for the small mammal species under study, an average home range (measured through Mimimum Convex Polygon method) for these species being around one ha (Stradiotto et al. 2009; Wolton 1985). Geographic attributes of islands (e.g. area, distance from the mainland, distance from the closest islands, etc.) were quantified through field measurements with the use of a GPS and aerial pictures taken in 2005.

On the mainland three sites of one hectare each were chosen (Table 2.1 and Figure 2.7). The distance between each island and the mainland was measured from the edge of the island to the right bank of the river and reported in meters. The six large islands were on average 154m distant from the mainland (range 11m to 280m), the eight medium islands were on average 113m from the mainland (range 25m to 311m), while the five small islands were on average 121m from the mainland (range 35m to 243m).

Figure 2.6 Study area photographed from Monte Ragogna in spring 2011. The red arrow indicates the direction of the flow, the black lines indicate the borders of the study area Photo: M. Zupan.

Table 2.1 List of islands that were studied, their area (in hectares), distance from the mainland (from the right bank), and class size (S = small; M = medium; L = large). N traps = number of Sherman traps; Tot Trap Nights = Number of traps x number of nights they were active for; N SS = Number of scent stations activated; Tot SS nights = Number of scent stations x number of nights they were active for; N Seasons = total number of seasons the scent stations were activated for. Sherman traps were active for four seasons, apart from I1 and I19 where neither traps nor scent stations were activated in winter (January 2011). On the mainland a total of 28 scent stations were activated along a unique continuous transect, as reported in Section 2.4.2.

ID	***Area (ha)***	***Distance (m)***	***Class size***	***N traps***	***Tot Trap nights***	***N SS***	***Tot SS nights***	***N seasons***
I1	0.17	25	M	3	27	1	40	3
I2	0.01	35	S	2	32	0	0	0
I3	0.01	58	S	2	32	0	0	0
I4	0.01	59	S	2	32	0	0	0
I5	1.72	223	L	13	208	2	33	4
I6	4.17	201	L	39	624	3	99	4
I7	0.59	311	M	4	64	1	33	4
I8	0.63	164	M	5	80	1	33	4
I9	1.80	149	L	13	208	2	66	4
I10	1.00	280	L	6	96	2	66	4
I11	0.43	43	S	3	48	1	33	4
I12	1.61	61	L	13	208	2	66	4
I13	0.84	175	S	6	96	1	33	4
I14	0.09	209	S	2	32	1	33	4
I15	0.10	243	S	2	32	1	33	4
I16	0.43	95	S	3	48	1	33	4
I17	0.67	54	S	5	80	1	33	4
I18	1.32	11	L	10	160	2	66	4
I19	0.92	36	S	6	54	1	22	3
M1	1	-	-	20	320			4
M2	1	-	-	20	320	28	924	4
M3	1	-	-	20	320			4

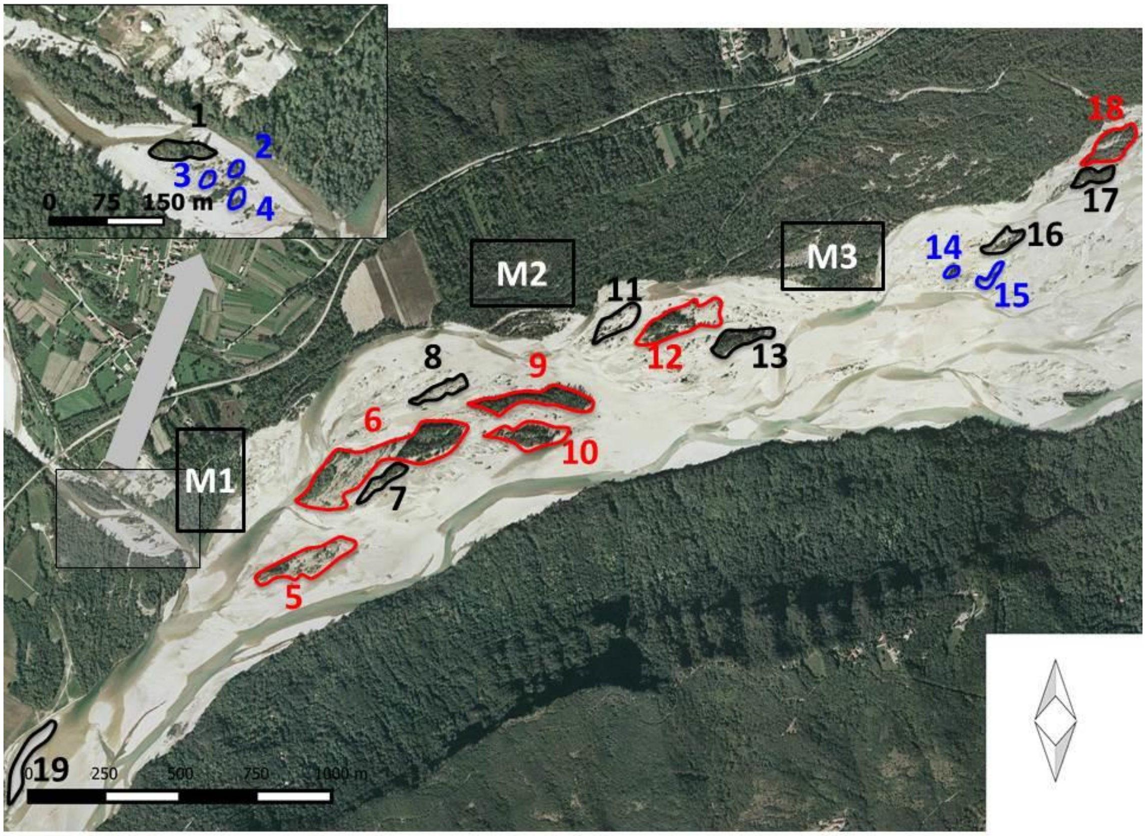


Figure 2.7 Location of the three mainland study sites and of the studied islands. Small islands are in blue; medium islands are in black; large islands are in red. The inset shows an enlarged section of the area where I1, I2, I3 and I4 are located.

2.3 The pilot study: choosing the focal species

This study was preceded by a one-year pilot study for a Master's thesis (Pavanello 2010) that helped inform the data collection of the present thesis. Pavanello (2010) investigated the small mammal composition and the carnivore community in a section of the river located within the study area of the present thesis. This pilot study involved the collection of data on a section of mainland approximately 2.5km long and on six of the islands that were also studied in the present thesis (I1, I6, I7, I9, I10 and I11 in Table 2.1). The study took place during four sampling sessions in December 2008, May 2009, August 2009 and October 2009. I contributed to the set-up of the study and the collection of the data throughout the pilot study.

To study the small mammal community, Pavanello (2010) used Sherman traps, open for four nights at a time. In December 2008, just three islands were trapped (i.e. I6, I9, I10) and on the mainland a single transect with 42 traps was laid down. In the following three trapping sessions (May–October) a total of 10 transects, four on the mainland and six on the islands, was organised. Traps were 20m apart. Each transect on the mainland contained 10 traps, while the number of traps on each island was proportional to island size from a minimum of two traps on the smallest island (I1, area= 0.17ha) to a maximum of 19 traps on the largest island (I6, area=4.17ha). Using this sampling strategy, Pavanello (2010) trapped 131 individuals of Wood mouse (*Apodemus sylvaticus),* 66 individuals of Striped field mouse (*Apodemus agrarius),* 48 individuals of Yellow necked mouse *(Apodemus flavicollis)*, nine individuals of the Common shrew (*Sorex araneus),* two Black rats (*Rattus rattus*), and one Water vole *(Arvicola amphibious italicus)* in a total of 1224 trap nights.

As far as the carnivores were concerned, both cage trapping and scent stations coupled with camera traps were used for their detection and identification. Two kinds of live traps were used: the smaller Whitlock traps spaced at a distance of 100m and larger cage traps spaced at a distance of 200m. A total of 50 Whitlock traps (35 on the mainland and 15 on the islands) and 18 cage traps (10 on the mainland and 8 on the islands) were set. The number of traps set on each island was proportional to island size, with a single trap placed on the smallest islands. A total of 19 scent stations were activated at the study area, with 200m spacings (8 on the mainland and 11 on the islands). On the islands number of scent stations was proportional to island size, with a minimum of one scent station on the smallest islands. Whitlock traps did not trap any carnivore species, while often trapping species of *Apodemus*, especially *A. agrarius*. Cage traps were activated for a total of 935 trap nights and the only species captured were the Stone marten (*Martes foina*) and *R. rattus* (Table 2.2). Scent stations were much more successful at detecting carnivores both on the mainland and on the islands (Table 2.2), even though they were set up for a comparable amount of nights to the traps (Scent stations were on for 893 trap nights).

Scent stations provided evidence for the occurrence of four carnivore species in the study area: Red fox (*Vulpes vulpes*), the Stone marten (*M. foina*), European badger (*Meles meles*) and a cat species (*Felis* spp.), showing different visiting rates in different seasons. *M. meles* and *Felis* spp. rarely visited the scent stations (two and six times respectively). Although it was not possible to distinguish whether the tracks belonged to the domestic cat (*Felis catus*) or to the wild cat (*Felis sylvestris*), a carcass of a shot wild cat was found on island I9 (Figure 2.8), providing evidence that river islands at the study site are visited by this species. Tracks of *V. vulpes* and *M. foina* were more frequently found, especially in autumn, probably due to the movements of dispersing juveniles. Of the three species, the most constant presence throughout the year was *V. vulpes* while *M. foina* was more present in autumn, when it made more appearances than *V. vulpes*.

Figure 2.8. A male wildcat (*F. sylvestris*) found shot at on an island in December 2008. Photo: F. Iordan.

Table 2.2 List of the carnivore species detected at the study area during the pilot study (reproduced with permission from Pavanello 2010). For the columns Traps and Camera traps, numbers indicate the total number of captures for each species. In the column Scent Stations, numbers indicate the total number of scent stations where tracks of carnivores were detected. "Other" stands for all the other non-carnivore species that were trapped or tracked (*Sus scrofa*, *Capreolus capreolus*, *Lepus europaea*, *R. rattus*, birds, dogs).

	Traps	*Scent Stations*	*Camera Traps*
Martes foina	7	97	10
Vulpes vulpes	0	27	0
Felis spp.	0	6	0
Meles meles	0	2	0
Other	10	102	2

The pilot study highlighted the species of small mammals and carnivores that were most abundant in the area and helped inform the selection of species for the present thesis. As this thesis is interested in studying the relationship between the landscape and mammal communities and populations, it was decided that it was important to choose species that were sufficiently abundant for these relationships to be explored. Hence, for small mammals, the research focused on the three *Apodemus* species found to have higher capture rates in the pilot study: *A. flavicollis*, *A. sylvaticus* and *A. agrarius.* For carnivores, data collection was focused on *M. foina* and *V. vulpes*, given the very few presences recorded for *M. meles* and *Felis spp*. during the pilot study.

The pilot study also highlighted that some trap nights were likely to be lost due to the Sherman traps being triggered by the Spanish slug (*Arion vulgaris*), especially in spring, summer and autumn (between 3% and 18% of trap nights were lost in each season in the pilot study). Therefore, in the present thesis, the number of Sherman traps on the smallest islands was increased to reduce the risk of trap failure.

2.4 Sampling protocol

Data collection on small mammals and carnivores was carried out during four sessions: May 2010 (spring session), September 2010 (summer session), November 2010 (autumn session) and January 2011 (winter session).

2.4.1 Small mammals

To study the factors affecting species diversity of *Apodemus* species on river islands and investigate whether there were differences in their life-histories between the mainland and the islands to address research questions N.1 and N.2 (chapter 3 and chapter 4), animals were live trapped. Sherman Traps (Sherman Tallahassee - FL, USA), baited with a mixture of rolled oats and wheat seeds were used. The bait was mixed personally. Traps were left in place for four days and checked early in the morning. On islands I1 and I19, traps were left in place for three nights in all seasons but were not activated in

January 2011. Captured animals were identified, marked using ear-tags (National Tag & CO – Newport, KY - USA) or fur clipping when they were too small to punch their ears, weighed to the nearest 0.5g with a Pesola spring balance, sexed, and their breeding condition noted. Females were recorded as imperforate, perforate, lactating, pregnant or having bred. Males were recorded as having abdominal testes or scrotal testes as an index of being respectively non reproductive or reproductive.

The trapping strategy was based on transects, following a protocol requiring a sampling effort (i.e. number of traps) proportional to the sampled area (Krebs 1999, p. 298). Proportional sampling was used because evidence exists that it can detect species-area relationships in landscape ecology studies more efficiently than uniform sampling (e.g. Schoereder et al. 2004). According to Pearson and Ruggero (2003), traps arranged in transects may sample more small mammal home ranges and encompass more and unique microhabitats in comparison to traps arranged in grids, therefore providing better information on community composition and better samples for examining demographic attributes.

Trap spacing in live-trapping studies depends on the population density and mobility/home range size of the study animal, which in turn varies between species and habitats (Tew et al. 1994). For example *A. sylvaticus* in unproductive arable habitats have home ranges of up to 8ha and are five times more wide-ranging and sparsely distributed than their woodland counterparts (Tew et al. 1994; Wolton 1985), requiring the trapping strategy in unproductive habitats to be based on greater inter-trap distances in respect to woodland habitats. Trap spacing distance used in this study was 20m. This distance represented a compromise between standard inter-trap spacing of 15m

(Montgomery 1985), in general used for trapping microtines in productive habitats like woodlands (Gurnell and Flowerdew 2006) and bigger distances used to trap more motile species (e.g. murids) inhabiting less productive habitats (Tew et al. 1994).

On the islands, the number of traps activated was proportional to island size (Table 2.1). The number of traps laid down on islands was chosen so as to trap a consistent portion of the area. Considering the trapping range of each trap as a circle around the trap with a diameter of 20m (i.e. the inter-trap distance), the number of traps set on each island was established as to trap a surface approximately equal to 25% of the area of each island. However, even though a single trap would have covered more than 100% of the area of the smallest islands (I2, I3, I4, I14 and I15), it was decided to increase the trapping effort on these islands using a minimum of two traps to reduce the probability of trap failure due to the Spanish slug (*Arion vulgaris*). On the mainland three sites were selected on the basis of the presence of trails which facilitated the transfers during the trapping periods (Figure 2.7): on each site two transects of 10 traps each were activated (Table 2.1), in each season.

To study the factors regulating the spatial dynamics of *A. agrarius* on the floodplain of the Tagliamento and address research question N.3 (chapter 5), a different trapping strategy was used based on grids instead of on transects. This is discussed in detail in chapter 5, sections 5.2.1 and 5.2.2.

For the small mammal study where trapping and handling of the animals was involved, the sampling protocols to collect field data on live captured animals was ethically evaluated and approved by the Italian Animal Care and Use Committee (Ministero dell'Ambiente e della Tutela del Territorio, Direzione per la Protezione della

Natura, Rome) and by the regional authorities (Direzione Centrale Risorse Agricole Forestali e Naturali, Regione Friuli Venezia Giulia), Number of Authorisation RAF 13/12.5/29602. The live-trapping techniques used were standard techniques approved by the Mammal Society (UK) and described in Gurnell and Flowerdew (2006). To minimize animal residence time in the traps, these were checked as early as possible in the morning. Traps were abundantly baited and well insulated with hay inside. On the outside they were covered with vegetation and, during the warmest months, placed in the shadow. Trap mortality was low with 35 individuals dying in traps out of 584 captures.

Genetic verification of small mammal species for doubtful cases

Two of the focal species are sometimes difficult to recognize with certainty based only on their morphological characteristics: *A. sylvaticus* and *A. flavicollis*. *A. sylvaticus* is closely related to *A. flavicollis* but differs in that it has a smaller or absent patch of yellow fur around the neck (Figure 2.9), has slightly smaller ears, and it is usually slightly smaller overall. In Central and Northern Europe, most adults of the two species can be easily discriminated because of the characteristic yellow patch of *A. flavicollis* (Lapini et al. 1995). However, in Southern Europe, *A. sylvaticus* also presents, at times, an elongated grey-yellowish patch (more long than broad) on the neck (Lapini et al. 1995) that makes the field discrimination with *A. flavicollis* on the basis of morphological characteristics alone more of a challenge (Capizzi and Filippucci 2008b).

Figure 2.9 Patches of yellow fur present on the neck of *A. flavicollis* (on the left) and of *A. sylvaticus* (on the right). Photo: F. Iordan.

Michaux et al. (2001) designed species-specific primers from the mitochondrial *cytochrome b* gene that allows these two *Apodemus* species to be rapidly and simply distinguished. The protocol was used with success in studies in southern Europe carried out in areas where the two species were syntopic and needed to be discriminated on a genetic basis (e.g. Mortelliti et al. 2009). Michaux et al. (2001) extracted the DNA from tissues of both *A. flavicollis* and *A. sylvaticus* individuals stored in ethanol and amplified a *Cytochrome b* fragment (1000 bp) using a polymerase chain reaction (PCR) through primers identified by Kocher et al. (1989). *Cytocrome b* fragments of 971 bp obtained were then sequenced and a pair of specific primers were designed for each species. Each pair of primers is used to amplify just the *Cytocrome b* fragment of one of the two species, allowing the discrimination between them. In the present study, there were 52 cases in which the discrimination between the two species was difficult, especially with juvenile individuals. In *A. flavicollis* the patch starts to be visible at around two weeks of age (Capizzi and Filippucci 2008b). For these individuals a sample was collected from the tail using a sterilized biopsy punch and then stored in 95% ethanol. After the extraction of the DNA from the tail, DNA Samples were then sent to the DNA Analytica Srl company in Trieste (Italy) where they were analysed following the protocol described above. A total of 47 individuals were identified as *A. sylvaticus* and five as *A. flavicollis*.

2.4.2 Carnivores

To explore the factors regulating carnivore use of the Tagliamento floodplain and infer some information regarding the potential predator pressure insisting on small mammal populations of the mainland and on the islands (chapter 6), scent stations were used. Trapping was not pursued because the pilot study highlighted that it was unlikely to add information about the carnivore community composition. Scent stations attracted carnivores through bait and recorded their presence using tracks and camera traps. Circular scent stations were prepared by mixing the local soil with a mixture of sand and clay. These components were manipulated to get a suitable substrate to record animal tracks. The relative proportion of sand : clay was approximately 1:2. Scent stations had a diameter of one meter and were created around a small tree which marked the centre of the circle and which acted as support for the bait.

Different kinds of baits and lure were tried, namely butcher discards, fish oil and diluted caproic acid, but butcher discards proved to be as successful as other baits tried, despite being the least expensive. Scent stations were positioned 200 meters apart and their number was proportional to island or mainland site size. On small and medium islands (area <1ha), just one scent station was set, while on large islands (area ≥1ha) two or three scent stations were set (Table 2.1). A total of 28 scent stations was activated on the mainland set along a continuous transect (Table 2.1). Scent stations were activated for a minimum of 6 to a maximum of 10 days in each season.

Given the problem of distinguishing among the tracks of some Mustelids like the polecat (*Mustela putorius*), the stone marten (*Martes foina*) and the pine marten (*Martes martes*), some camera traps (Scout Guard SG 550) were set at the scent stations immediately after an equivocal track was found. This allowed the filming or photographing of the animals that visited the scent stations, helping with their identification. Further details about the methodology used to prepare scent stations and to attract carnivores are reported in chapter 6 section 6.2.2.

2.5 Mammal species recorded on the Tagliamento

Data on signs of mammal presence (e.g. tracks and faeces) found outside the scent stations or nearby traps during the field campaigns were recorded. Scent stations, faeces/tracks collection and trapping proved the occurrence of 19 species of mammals within the study area, including 15 species recorded on islands (Table 2.3). The community of mammals inhabiting the Tagliamento appeared to be composed mainly of riparian generalists which make periodical use of riparian habitats just for some of the activities of their life cycle; the only riparian obligate found was the Water vole (*A. amphibius italicus).* The three most abundant small mammal species recorded in the study area were *A. agrarius*, *A. sylvaticus* and *A. flavicollis.* Among carnivores the most abundant species recorded were *M. foina* and *V. vulpes*.

Table 2.3 Mammal species recorded in the study area (NR= not recorded, obs= observed, CT= revealed by camera trap, LT=live trapped).

	MAINLAND						ISLANDS					
SPECIES	*NR*	*obs*	*tracks*	*feaces*	*CT*	*LT*	*NR*	*obs*	*tracks*	*feaces*	*CT*	*LT*
Cervus elaphus	●								●			
Vulpes vulpes		●	●	●	●				●	●	●	
Meles meles			●						●			
Martes foina			●	●	●	●			●	●	●	●
Felis sylvestris	●							●				
Sus scrofa		●	●	●					●	●		
Myocastor coypus		●	●	●					●			
Capreolus capreolus		●	●	●				●	●	●		
Lepus europaeus	●							●	●	●		
Sciurus vulgaris			●			●	●					
Rattus rattus						●	●					
Myodes glareolus						●						●
Apodemus sylvaticus						●						●
Apodemus agrarius						●						●
Apodemus flavicollis						●						●
Arvicola amphibius italicus	●											●
Sorex aranaeus						●	●					
Crocidura suaveolens						●						●
Erinaceus concolor			●				●					

2.6 Focal species

2.6.1 Apodemus flavicollis: general biology

The yellow necked mouse (*A. flavicollis*) belongs to the rodent family Muridae. Its range includes the more mountainous parts of Western Europe with the exception of northern Scandinavia, southern Spain and western France. This mouse occurs in Great Britain but not in Ireland, and it is also absent from a number of Mediterranean islands (e.g. Sardinia, Sicily, Corsica). In Asia, its range extends eastward to the Ural Mountains (Amori et al. 2008). Localised studies suggest that *A. flavicollis* is a habitat specialist mainly associated with mature deciduous woodland (Gurnell 1985; Montgomery 1985; Yalden 1971) and with woodland areas displaying a wide diversity of seed-bearing tree species (Yalden and Shore 1991). In coppice woodland *A. flavicollis* is the only rodent to prefer older, more established compartments, while it is seldom recorded in recent coppice (Capizzi and Luiselli 1996). It is mainly a granivore species, with animal food (insects) becoming more frequent in the diet in spring and summer (Holisova and Obrtel 1980; Obrtel and Holisova 1983). Maximum life span in a wild population is two years, but few individuals live more than one year (Corbet and Harris 1991).

In northern European populations, the breeding season occurs between February-March and October, with some rare examples of winter reproduction usually associated with large mast crops (Stenseth et al. 2002). In Mediterranean areas reproduction in winter happens more frequently and a high number of juveniles are usually captured in spring. Reproduction is usually anticipated of 2-8 weeks in areas where the species coexists with *A. sylvaticus* (Montgomery 1980). Mean litter size is 5.0-6.8 and up to three litters can be produced in a year (Flowerdew 1985).

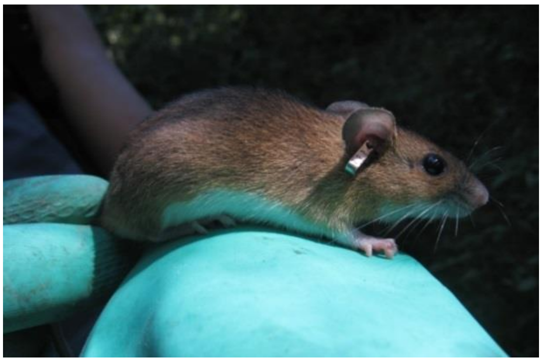


Figure 2.10 *A. flavicollis* captured and ear tagged in the study area. Photo: F. Iordan.

2.6.2 Apodemus sylvaticus: general biology

The wood mouse (*A. sylvaticus*), is a common murid rodent. In Europe it ranges north to Scandinavia and east to Ukraine but it is also found in North-western Africa and on many Mediterranean islands (IUCN 2008a).

A. sylvaticus is a habitat generalist that inhabits all stages of forest succession (Flowerdew 1985; Gurnell 1985; Watts 1969), agricultural land (Tattersall et al. 1997) and even sand dunes (Corp et al. 1997). Some authors found the species in greater abundance in areas with good low level cover (Fitzgibbon 1997), while others found this relationship does not exist (Gurnell 1985). It is an opportunist granivorous species, able to feed on seeds all year long with peaks in autumn, when this food can constitute up to the 75% of the diet. Green parts of plants are consumed mainly in summer and autumn. Animal food (e.g. *Laepidottera* larvae) assumes low importance in the diet of this species, with peaks in consumption in spring when it can represent 10% of the diet (Watts 1968).

In central and northern Europe, reproduction peaks in summer with an interruption or a marked reduction in winter (Smal and Fairley 1982); in Mediterranean countries, reproductive activity extends from late summer or early autumn until spring (Moreno and Kufner 1988). Average litter size is usually 4.5-6.5 (Flowerdew 1985). In conditions of syntopy with *A. flavicollis,* there could be an anticipated reproduction and/or a reduction of the proportion of reproductive individuals in the population (Flowerdew and Ellwood 2001; Montgomery 1981).

Figure 2.11 Male and female of *A. sylvaticus* captured in the same trap at the study site. Photo: F. Iordan.

2.6.3 Apodemus agrarius: general biology

The striped field mouse (*A. agrarius*) is a rodent of the family Muridae. The range of this species stretches from Eastern Europe to Korea, including Taiwan and Siberia. In Italy it is present in the flat areas of the North-east, with some populations found also in the provinces of Milan and Pavia (Capizzi and Filippucci 2008a). Seeds and fruits constitute the bulk of the diet, which includes also herbs, buds and animal food (Gliwicz 1984; Holisova 1967).

A. agrarius is a species typical of the agricultural field-forest habitat mosaic (Kozakiewicz et al. 1999). It occupies a great variety of plain habitats. It is usually found in fringes of woodland and scrub, agricultural areas and hedgerows, often associated with damp areas and river valleys (Zulian 1987). According to Zeida (1967), in central Europe the species occupies different habitats depending on the density of its populations: in conditions of low-average densities, the species is common in riparian forests, while at high densities, the species colonizes also agricultural fields and cereals, woodlands and meadows.

Reproduction starts in early spring and extends up to September in central Europe, while in the southern part of the range may last longer (Andrzejewski et al. 1978). Individuals reach sexual maturity at two months of age. Litter size varies between three and nine. Usually females give birth three-four times per year.

Competition with *A. flavicollis* and *M. glareolus* in woodland ecosystems has been found, given the similarity of the food niche among the three species: when the three species coexist in the same area, density of *A. agrarius* decreases as a consequence of (1) aggressive interactions between individuals, (2) higher mortality rates of adults and juveniles, and (3) higher migration rates of sexually mature individuals (Gliwicz 1984; Kozakiewicz and Boniecki 1994).

Figure 2.12 *A. agrarius* captured and ear tagged at the study site. Photo: F. Iordan.

2.6.4 Martes foina: general biology

The stone marten (*M. foina*) is a carnivore species belonging to the family Mustelidae, subfamily Mustelinae. It is native of central and Western Europe and Central Asia, though it has also established a feral population in North America. The species is absent in the UK, Iceland, Scandinavia and in almost all of Russia (IUCN 2008b).

M. foina is a generalist and adaptable species, occurring in a number of open and forest habitats and also in urban areas (Delibes 1983). In some individuals a marked preference for anthropic infrastructures (barns, haylofts and attics) has been noted (Genovesi 2003). The great plasticity and adaptability of this species to different habitats is also reflected in its opportunist diet, which varies among seasons and geographical areas (Genovesi et al. 1996). Fruit contributes significantly to the diet of the species; indeed, *M. foina* is the most frugivorous species among European carnivores (Pandolfi et al. 1996). Another important source of food is represented by rodents: mice, voles, rats and also young hares and rabbits. *M. foina* also eats birds and their eggs, frogs, lizards and insects (Genovesi et al. 1996).

M. foina has a reproductive strategy characterized by embryonic diapause. Gestation lasts 28-30 days and cubs are usually born between the end of March and beginning of April. Litter size is 3-7, depending on the age of the female (Mead and Wright 1983). The species has always been described as a solitary species, which hunts individually (Powell 1994). Available data on the species' spatial behaviour, show that home ranges of males can overlap with those of one or more females (e.g. Skirnisson 1986) and sub-adults are usually tolerated in the parent’s home range, but that range overlap with the same sex is limited (Genovesi and Boitani 1995).

Figure 2.13 A stone marten (*M. foina*) captured and released in the study area. Photo: M. Pavanello.

2.7 References

Amori, G., Hutterer, R., Kryštufek, B., Yigit, N., Mitsain, G., Palomo, L.J., 2008. Apodemus flavicollis. The IUCN Red List of Threatened Species. Version 2014.2.

Capizzi, D. and Filippucci, M.G., 2008a. Apodemus agrarius, In Fauna d'Italia. Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia. eds G. Amori, L. Contoli, A. Nappi. Calderini, Milano.

Capizzi, D. and Filippucci, M.G., 2008b. Apodemus flavicollis, In Fauna d'Italia. Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia. eds G. Amori, L. Contoli, A. Nappi. Calderini, Milano.

Capizzi, D. and Luiselli, L., 1996. Ecological relationships between small mammals and age of coppice in an oak-mixed forest in central Italy. Rev. Ecol. (Terre et Vie) 51, 277-291.

Corbet, G.B., Harris, S., 1991. The Handbook of British Mammals, 3th Edition. Blackwell Scientific Publications, Oxford.

Corp, N., Gorman, M.L., Speakman, J.R., 1997. Ranging behaviour and time budgets of male wood mice Apodemus sylvaticus in different habitats and seasons. Oecologia 109, 242-250.

Delibes, M., 1983. Interspecific competition and the habitat of the stone marten Martes foina (Erxleben 1777) in Europe. Acta Zoologica Fennica 174, 229-231.

Edwards, P.J., Kollmann, J., Gurnell, A.M., Petts, G.E., Tockner, K., Ward, J.V., 1999. A conceptual model of vegetation dynamics on gravel bars of a large Alpine river. Wetlands Ecology and Management 7, 141-153.

Fitzgibbon, C.D., 1997. Small mammals in farm woodlands: The effects of habitat, isolation and surrounding land-use patterns. Journal of Applied Ecology 34, 530-539.

Flowerdew, J.R., 1985. The population dynamics of wood mice and yellow necked mouse. Symposia of the Zoological Society of London 55, 315-338.

Flowerdew, J.R. and Ellwood, S.A., 2001. Impact of woodland deer on small mammal ecology. Forestry 74, 277-287.

Francis 2007. Size and position matter: riparian plant establishment from fluvially deposited trees. Earth Surface Processes and Landfroms 32, 1239-1243.

Francis, R.A., Tibaldeschi, P., McDougall, L., 2008. Fluvially-deposited large wood and riparian plant diversity. Wetlands Ecology and Management 16, 371-382.

Genovesi, P., 2003. Faina (Martes foina), In Fauna d'Italia Mammalia: Carnivora Artiodactyla. eds L. Boitani, S. Lovari, A. Vigna Taglianti (eds), pp. pp 113-223. Calderini, Bologna.

Genovesi, P. and Boitani, L., 1995. Preliminary data on the social organization of the Stone marten (Martes foina, Erxl., 1777) in Tuscany. Hystrix 7, 159-163.

Genovesi, P., Secchi, M., Boitani, L., 1996. Diet of the stone marten: an example of ecological flexibility. Journal of Zoology, London 238, 545-555.

Gliwicz, J., 1984. Competition among forest rodents: effects of Apodemus flavicollis and Clethrionomys glareolus on A. agrarius. Acta Zoologica Fennica 172, 57-60.

Gurnell, A.M., Petts, G.E., Hannah, D.M., Smith, B.P.G., Edwards, P.J., Kollmann, J., Tockner, K., 2001. Riparian vegetation and island formation along the gravel-bed Fiume Tagliamento, Italy. Earth Surface Processes and Landforms 26, 31-62.

Gurnell, A. and Petts, G., 2006. Trees as riparian engineers: the Tagliamento river, Italy. Earth Surface Processes and Landforms 31, 1558-1574.

Gurnell, J., 1985. Woodland rodent communities. Symposia of the Zoological Society of London 55, 377-411.

Gurnell, J. and Flowerdew, J. R., 2006. Live Trapping Small Mammals 4th edition. The Mammal Society London UK.

Holisova, V., 1967. The food of Apodemus agrarius (Pall.). Zool. Listy 16, 1-14.

Holisova, V. and Obrtel, R., 1980. Food resource partioning among four myomorph rodent populations coexisting in a spruce forest. Folia Zoologica 29, 193-207.

IUCN, 2008a. Apodemus sylvaticus. The IUCN Red List of Threatened Species. Version 2014.2.

IUCN, 2008b. Martes foina. The IUCN Red List of Threatened Species. Version 2014.2.

Karrenberg, S., Kollmann, J., Edwards, P.J., Gurnell, A., Petts, G.E., 2003. Basic and applied ecology patterns in woody vegetation along the active zone of a near natural alpine river. Basic and Applied Ecology, 4, 157-166.

Katulic, S., 2003. Kleinsauger in unterschedlichen Habitattypen in Flussauen (Thur/Tagliamento), In Department Biologie. p. 87. Eidgenössische Technische Hochschule Zürich (ETHZ), Duberdorf.

Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Paabo, S., Villablanca, F.X., Wilson, A.C., 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences of the USA 86, 6196-6200.

Kollmann, J., Vieli, M., Edwards, P.J., Tockner, K., Ward, J.V., 1999. Interaction between vegetation developement and island formation in the Alpine river Tagliamento. Applied Vegetation Science, 25-36.

Kozakiewicz, A. and Boniecki, P., 1994. Intra-and interspecific behaviours in bank vole and striped-field mouse under enclosure conditions. Acta Theriologica 39, 29-36.

Kozakiewicz, M., Gortat, T., Kozakiewicz, A., Barkowska, M., 1999. Effects of habitat fragmentation on four rodent species in Polish farm landscape. Landscape Ecology 8, 29-36.

Krebs, C.J., 1999. Ecological Methodology, 2nd ed. Addison-Welsey Educational Publishers, Menlo Park, CA, 620pp.

Lapini, L., 2009. Small mammals of the Natural Reserve lake of Cornino (Forgaria del Friuli, Udine, North-Eastern Italy). . Gortania-Atti Museo Friulano di Storia Naturale 31, 145-172.

Lapini, L., Dall'Asta, A., Dublo, L., Spoto, M., Vernier, E., 1995. Materiali per una teriofauna dell'Italia Nord-orientale (Mammalia, Friuli-Venezia Giulia). Gortania 17, 149-248.

Lippert, W., Mueller, N., Rossel, S., Schauer, T., Vetter, G., 1995. Der Tagliamento-Flussmorphologie und auenvegetation der grossten wildflusslandschaft in den Alpen. Jahrbuch des Vereins zum Schutz der Bergwelt 60, 11-70.

Mardhiah, U., Rillig, M.C., Gurnell, A., 2015. Reconstructing the development of sampled sites on fluvial island surfaces of the Tagliamento River, Italy, from historical sources. Earth Surface Processes and Landforms 40, 629-641.

Mead, R.A. and Wright, P.L., 1983. Reproductove cycles of Mustelids. Acta Zoologica Fennica 174, 169-172.

Michaux, J.R., Kinet, S., Filippucci, M.G., Libois, R., Besnard, A., Catzeflis, F., 2001. Molecular identification of three sympatric species of wood mice (Apodemus sylvaticus, A. flavicollis, A. alpicola) in western Europe (Muridae: Rodentia). Molecular Ecology Notes 1, 260-263.

Montgomery, W.I., 1980. Spatial organization in sympatric populations of Apodemus sylvaticus (L.) and A. flavicollis (Rodemtia, Muridae). Journal of Zoology 192, 351-377.

Montgomery, W.I., 1981. A removal experiment with sympatric populations of Apodemus sylvaticus (L.) and A. flavicollis (Melchior) (Rodentia: Muridae). Oecologia 51, 123-132.

Montgomery, W.I., 1985. Interspecific competition and the comparative ecology of two congeneric species of mice, In Case Studies in Population Biology. ed. L.M. Cook, pp. 126-187. Manchester University Press, Manchester.

Montgomery, W.I. and Gurnell, J., 1985. The behaviour of Apodemus. Symposia of the Zoological Society of London 55, 89-108.

Moreno, S. and Kufner, M.B., 1988. Seasonal patterns in the Wood mouse population in Mediterranean Scrubland. Acta Theriologica 33, 79-85.

Mortelliti, A., Amori, G., Annesi, F., Boitani, L., 2009. Testing for the relative contribution of patch neighborhood, patch internal structure, and presence of predators and competitor species in determining distribution patterns of rodents in a fragmented landscape. Canadian Journal of Zoology 87, 662-670.

Obrtel, R. and Holisova, V., 1983. Winter and spring diet of three coexisting Apodemus species. Folia Zoologica 32, 291-302.

Pandolfi, M., De Marinis, A.M., Petrov, I., 1996. Fruit as a winter feeding resource in the diet of stone marten (Martes foina) in east-central Italy. Zeitschrift fur Saugetierkunde 61, 215-220.

Pearson, D.E. and Ruggiero, L.F., 2003. Transect versus grid trapping arrangements for sampling small-mammal communities. Wildlife Society Bulletin 31, 454-459.

Powell, R.A., 1994. Structure and spacing of Martes populations, In The biology and conservation of-martens, sables and fishers. eds S.W. Buskirk, A.S. Harestad, M.G. Raphael, R.A. Powell. Cornell University Press, Ithaca, New York.

Schoereder, J.H., Galbiati, C., Ribas, C.R., Sobrinho, T.G., Sperber, C.F., DeSouza, O., Lopes-Andrade, C. 2004. Should we use proportional sampling for species-area studies? Journal of Biogeography 31, 1219-1226.

Skirnisson, K., 1986. Untersuchungen zum Raumzeit-system freilebender Steinmarder (Martes foina Erxleblen, 1777). Beitr. Wildbiol. 6, 1-200.

Smal, C.M. and Fairley, J.S., 1982. The dynamics and regulation of small rodent populations in the woodland ecosystems of Killarney, Ireland. Journal of Zoology 196, 1-30.

Stenseth, N.C., Viljugrein, H., Jedrzejewski, W., Mysterud, A., Pucek, Z., 2002. Population dynamics of Clethrionomys glareolus and Apodemus flavicollis: Seasonal components of density dependence and density independence. Acta Theriologica 47, 39-67.

Stradiotto, A., Cagnacci, F., Delahay, R., Tioli, S., Nieder, L., Rizzoli, A., 2009. Spatial organization of the yellow-necked mouse: Effects of density and resource availability. Journal of Mammalogy 90, 704-714.

Tattersall, F.H., Macdonald, D.W., Manley, W., Gates, S., Feber, R., Hart, B.J., 1997. Small mammals on one-year set-aside. Acta Theriologica 42, 329-334.

Tew, T.E., Todd, I.A., Macdonald, D.W., 1994. The effects of trap spacing on population estimation of small mammals. Journal of Zoology 233, 340-344.

Tockner, K., Ward, J.V., Arscott, D.B., Edwards, P.J., Kollmann, J., Gurnell, A.M., Petts, G.E., Maiolini, B., 2003. The Tagliamento river: a model ecosystem of European importance. Aquatic Science 65, 239-253.

Ward, J.V., Tockner, K., Edwards, P.J., Kollmann, J., Bretschko, G., Gurnell, A., Petts, G.E., Rossaro, B., 1999. A reference river system for the Alps: the fiume Tagliamento. Regulated rivers: research & management 15, 63-75.

Watts, C.H.S., 1968. The Foods Eaten by Wood Mice (Apodemus sylvaticus) and Bank Voles (Clethrionomys glareolus) in Wytham Woods, Berkshire. Journal of Animal Ecology 37, 25-41.

Watts, C.H.S., 1969. The Regulation of Wood Mouse (Apodemus sylvaticus) numbers in Wytham Woods, Berkshire. Journal of Animal Ecology 38, 285-304.

Wolton, R.J., 1985. The ranging and nesting behaviour of Wood mice, Apodemus sylvaticus (Rodentia:Muridae), as revealed by radio-tracking. Journal of Zoology 206, 203-224.

Yalden, D.W., 1971. A population of the Yellow-necked mouse, Apodemus flavicollis. Journal of Zoology 164, 244-250.

Yalden, D.W. and Shore, R.F., 1991. Yellow necked mice Apodemus flavicollis at Woodchester Park, 1968-1989. Journal of Zoology 224, 329-332.

Zanoni, L., Gurnell, A.M., Drake, N., Surian, N., 2008. Island dynamics in a braided river from an analysis of historical maps and air photographs. River Research and Applications, 24, 1141-1159.

Zulian, E., 1987. Reperti sulla distribuzione e sulla biologia di Apodemus agrarius (Pallas) (Rodentia Muridae) nell’Italia nord-orientale. Lavori - Società veneziana Scienze naturali 12, 133-147.

Chapter 3 - Influence of scale-dependent factors in regulating small mammal assemblages in a semi-natural riparian landscape

Abstract

Landscape ecology studies the influence of spatial patterns on ecological processes and on biodiversity. It considers the ecological consequences of where things are located in space, where they are relative to other things, and how these relationships and their consequences depend on the characteristics of the surrounding landscape mosaic, at multiple scales in time and space.

In this chapter, a landscape ecology approach was used to investigate how different variables describing landscape structure and landscape dynamism affect small mammal diversity in the context of an island-braided section of the River Tagliamento. Four variables and their reciprocal interactions were investigated in their role of shaping the small mammal diversity of Tagliamento islands, namely island area, island degree of isolation, number of floods insisting on islands and seed species diversity, a proximate factor for measuring food availability for small mammals. The approach used to study the interaction of these variables was Path Analysis.

Results suggest that small mammal diversity on islands was regulated by the concurrent influence of island area, seed species diversity and number of floods insisting on islands (i.e. degree of disturbance islands are subjected to). These variables interact in a particular way within the context of the Tagliamento floodplain. Area and seed species diversity showed a direct positive effect on small mammal diversity, which increased as these variables increased in their values. Area was also shown to influence small mammal diversity in an indirect way, by regulating the number of the times each island had been flooded in the course of the year: the bigger the island area, the lower the number of times an island was inundated and also the higher the small mammal diversity.

Results are discussed explaining how variables acting at the patch scale (area and seed species diversity) and at the landscape scale (number of floods) individually and simultaneously interact to regulate the diversity of small mammals in the context of the highly heterogeneous landscape of the Tagliamento riparian mosaic.

3.1 Introduction

Landscape ecology deals with the influence of spatial patterns on ecological processes and on biodiversity (Turner 1989). It considers the ecological consequences of where things are located in space, where they are relative to other things, and how these relationships and their effects depend on the characteristics of the surrounding landscape mosaic, at multiple scales in time and space. Over recent decades landscape ecologists have brought into question the traditional concept that considers streams and rivers as linear components of complex and heterogeneous landscape mosaics (Forman and Godron 1981) and have proposed a new view that considers streams and rivers themselves as complex and heterogeneous landscapes (Malard et al. 2002; Ward 1998; Ward et al. 2002; Wiens 2002). According to this view, rivers have an internal structure of their own represented by the pattern of pools and riffles of a small stream, the channels and vegetated islands of a braided river in a floodplain, or the main stem, backwaters, and oxbows of a large river. Landscape ecology can therefore provide an effective framework for the study of riverine ecosystems and consequently these systems may provide excellent opportunities to test landscape ecological tenets (Ward et al. 2002).

In this chapter, a landscape ecology approach was used to investigate how different variables describing landscape structure affect small mammal species diversity in the context of an island-braided section of the River Tagliamento.

The landscape mosaic and its characteristcs are influential in determining species presence and persistence (Kupfer et al. 2006) and therefore species distribution and diversity. The distribution and diversity of small mammal species in a given habitat constituting a landscape are known to be highly sensitive to variation in biotic variables like local vegetation structure and diversity which in turns affects diversity of available food (e.g. Cockburn and Lidicker 1983; Holland and Bennett 2007; Miller and Getz 1977). Furthermore, type of ground cover has been shown to substantially affect small mammal diversity and richness: for example small mammals may avoid bare ground or short grass habitats (Scott et al. 2008), where the predation risk is potentially higher (Eccard et al. 2000, Tattersall et al. 2001). Variables operating at different spatial scales will affect small mammal dynamics (Diffendorfer et al. 1999): at a local scale (e.g. within a single habitat patch), ecological processes like births and deaths, demographic stochasticity and competition are known to affect species distribution, abundance and diversity (Bowers and Dooley 1991). Alongside this, local spatial attributes like patch area are well known to affect species diversity and abundance of small mammals (e.g. Fitzigibbon 1997, Nupp and Swihart 2000; Pardini et al. 2005). However, the species diversity and distribution of a given patch may also be determined by variables operating at a landscape scale, for example by the degree of isolation/connectivity of that patch and of the surrounding ones (Kozakiewicz et al. 1999), combined with the dispersal capabilities of individual species (Diffendorfer et al. 1999; Nupp and Swihart 2000). The dispersal of individuals between distinct populations (i.e. immigration to a new patch and emigration from a patch), together with extinction due to stochastic events may indeed strongly affect local species diversity (Hanski 1986; Peltonen et al. 1989; Robinson et al. 2002).

Stochastic events and disturbances that can lead to habitat fragmentation may also cause alterations in landscape structure, reduce species competition and change resource availability (Sher et al. 2000), thereby altering the species diversity of a given landscape in complex ways. In a study on small mammals carried out in the Atlantic rainforest of southern Brazil, habitat fragmentation caused by anthropic disturbance increased environmental heterogeneity of the whole landscape: this in turn reduced the effects of inter-specific competition and enabled coexistence of a larger number of ecologically similar species, if compared with the number of species inhabiting that landscape prior to fragmentation happened (Conda and Rocha 2006).

Within this context, it is interesting to analyse how different variables acting at patch and landscape scales interact to determine small mammal diversity on the River Tagliamento, as the floodplain of this river shows a high degree of spatial and habitat heterogeneity (Gurnell et al. 2005) and is periodically subject to stochastic disturbances represented by floods. It was predicted that small mammal species diversity on river islands of the Tagliamento was regulated by the area and the spatial context of islands and also by the availability of food resources for small mammals (subsidising mechanisms of interspecific competition) and by their ephemeral nature due to periodic disturbance.

From the 1990s, small mammal taxa have been used to explore how dynamics occurring at patch and landscape scale affect species diversity of animals. The kind of landscapes which have been investigated up to now are remnant forest fragments (e.g. Gascon et al. 1999; McShea et al. 2003), small woodlots interspersed in a matrix of agricultural fields (e.g. Bowman et al. 2001; Fitzgibbon 1997; Kozakiewicz et al. 1999; Mortelliti et al. 2009; Nupp and Swihart 2000; Van Apeldoorn et al. 1992), experimental landscapes (e.g. Bowers et al. 1996; Collins and Barrett 1997; Diffendorfer et al. 1995), or other patchy remnant habitats in coastal environments (e.g. Bolger et al. 1997) and mountaintops (Frey et al. 2007). No studies have applied key principles of landscape ecology to investigate small mammal diversity and community structure in a semi-natural riparian landscape characterized by the presence of river islands.

The strength of the approach proposed here lies in the array of variables that have been considered and how they individually interact to affect species diversity of small mammals on the islands of the River Tagliamento.

3.2 Methods

3.2.1 Study area and species under study

The present study was conducted in a braided section of the River Tagliamento. For a detailed description of the study area, of the vegetation community and of the mechanism of island formation, see chapter 2, sections 2.1-2.2 and Figure 2.7.

Data were collected on 17 established islands, ranging in area between 0.01ha and 4.17ha (islands I2-I18 in Table 2.1, section 2.2 in chapter 2). These islands differed in their vegetation composition (i.e. in the percentage of vegetation cover and in the composition of the shrub layer) and varied in their spatial context (e.g. degree of isolation and area). Three species of small mammals that showed the highest capture rates in the study area were selected for investigation: *Apodemus agrarius*, *Apodemus sylvaticus* and *Apodemus flavicollis*. For a detailed description of the biology and ecology of the three *Apodemus* species, see chapter 2, sections 2.6.1-2.6.3.

A. sylvaticus and *A. flavicollis* in Southern Europe are at times difficult to distinguish because individuals of *A. sylvaticus* also presents, at times, an elongated grey-yellowish patch (more long than broad) on the neck (Lapini et al. 1995) that makes the field discrimination with *A. flavicollis* on the basis of morphological characteristics alone more of a challenge (Capizzi and Filippucci 2008). In order to assign controversial phenotypes of *A. sylvaticus* and *A. flavicollis*, a small sample of the end of the tail was collected and genetic analyses were performed following the protocol of Michaux et al. (2001). After the extraction of the DNA from the tail, DNA samples were sent for amplification and species identification to the genetic lab of DNA Analytica Srl – University of Trieste (Italy). The protocol for DNA amplification and species identification is described in detail in chapter 2, section 2.4.1. This sample collection was authorised by the Region Friuli Venezia Giulia under Authorisation Number RAF 13/12.5/29602.

3.2.2 Small mammal trapping and estimation of small mammal diversity

Sherman traps (Sherman - Tallahassee, FL - USA) were placed in each of the sampled islands. Traps were set 20m apart and were filled with hay and baited with a mixture of rolled oats and sunflower seeds. For estimates of species diversity and abundance to be comparable, the number of traps was proportional to island size from a minimum of two traps on the smallest islands, to a maximum of 39 traps on the largest island. Traps were left in place for three-four days and checked daily early in the morning (Gurnell and Flowerdew 2006). Animals trapped were individually marked using ear-tags (National Tag & CO – Newport, KY - USA), weighed and sexed. Four sessions of trapping were carried out in 2010/2011, one in each season: May 2010 (spring session), September 2010 (summer session), November 2010 (autumn session) and January 2011 (winter session).

In order to estimate *small mammal diversity* for each island, the Shannon-Wiener function (Kent and Coker 1992) was used. This index takes into account not only the number of species at a given location, but also the proportion of the total sample belonging to the *i*th species, therefore providing an indication of the community structure at the given location. For the calculation of this index, the *annual* *population density* of each species on each island was used, therefore directly taking into account trapping effort on each island. Indeed, *annual population density* was calculated for each of the three considered species by averaging the seasonal population density of each species on each island (*island seasonal density, ISD*). During the course of the study some trap nights were lost due to the traps being triggered by other species, especially by the Spanish slug (*Arion vulgaris*) in spring, summer and autumn. The index of *ISD* took into account these false triggers and was calculated as:

$$ISD = \frac{N\ captures\ zi\ \ captured\ on\ xi\ \ in\ yi}{TE\ \ on\ xi\ in\ yi} \times\ 100$$

Where:

ISD= island seasonal density

z_i = species (*A. flavicollis*, *A. sylvaticus*, *A.agrarius*)

$x_{i\,=}$ island

$y_{i\,=}$ season (spring, summer, autumn, winter)

TE= Trapping Effort = (trap nights carried out) – (trap nights lost due to false triggers)

This index takes trapping effort into account and hence makes the resulting estimates of population densities between different islands comparable. The fact that there were only two traps on small islands could have lead to trap saturation and to a reduced ability to correctly estimate small mammal diversity on these islands. Of the five islands where there were only two traps, trap saturation was observed on 20 cases out of a total of 80 total cases of trapping (i.e. 25%), where one case is one night of trapping on one island that has only two traps. This means that there were 60 days in which there was at least one trap open and available for trapping. On I4 trap saturation occurred in 50% of total cases, on I2, I3 and I14 in 25% of cases, and on I15 it never occurred. Therefore it can be concluded that trap saturation was not an issue as there were many days in which there were traps open and available for trapping.

3.2.3 Explanatory variables describing islands attributes

Islands were characterized according to their biotic, abiotic and spatial attributes (variables *hereafter*), derived from field surveys and available GIS data sets. Variable type, scale (island or landscape), mean values and ranges are reported in Table 3.2.

Biotic and abiotic variables

- *Seed species diversity* – Field surveys were conducted to record tree and shrub species carrying soft and hard seeds and their percentage cover on the islands. Cover of tree and shrub species carrying seeds was measured according to Braun-Blanquet classes using random positioned 10 x 10m quadrants. Proportional to island size, up to 13 quadrants were sampled in each of the studied islands. Quadrant data were collected in late summer 2010 for all islands. The following seed carrying species were dominant in the study area: *Acer* sp., *Cornus sanguinea*, *Corylus avellana*, *Crataegus* sp., *Fraxinus* sp., *Juglans nigra*, *Prunus* sp., *Rubus* sp., *Quercus* sp. As an index of seed species diversity, the Shannon-Wiener function following Kent and Coker (1992) was calculated for each 10x10m quadrant and a mean value was obtained for each island by averaging the values obtained for each quadrant.
- *Floods* – Flooding represents the major physical disturbance along river corridors which consist in intense water level changes. Rivers also experience frequent but smaller water level fluctuations called flow pulses (Tockner et al. 2000), that occurr

well below the bankfull discharge. In this study floods are defined as disturbance events which involve complete inundation of the floodplain, usually occurring on the Tagliamento three-four times per year in spring and autumn (Tockner et al. 2003). During the study period two big floods occurred in early November and in late December and other lighter floods happened in May, August and October 2010 (Figure 3.1). Data on the number of times each island was flooded was recorded through surveys on the islands after floods and photographic analysis of pictures taken through an automatic camera positioned on the Monte of Ragogna, in front of the study area. An island was considered flooded (i.e. disturbed) when immediately after a flood it showed wet ground, fallen trees or flattened grasses.

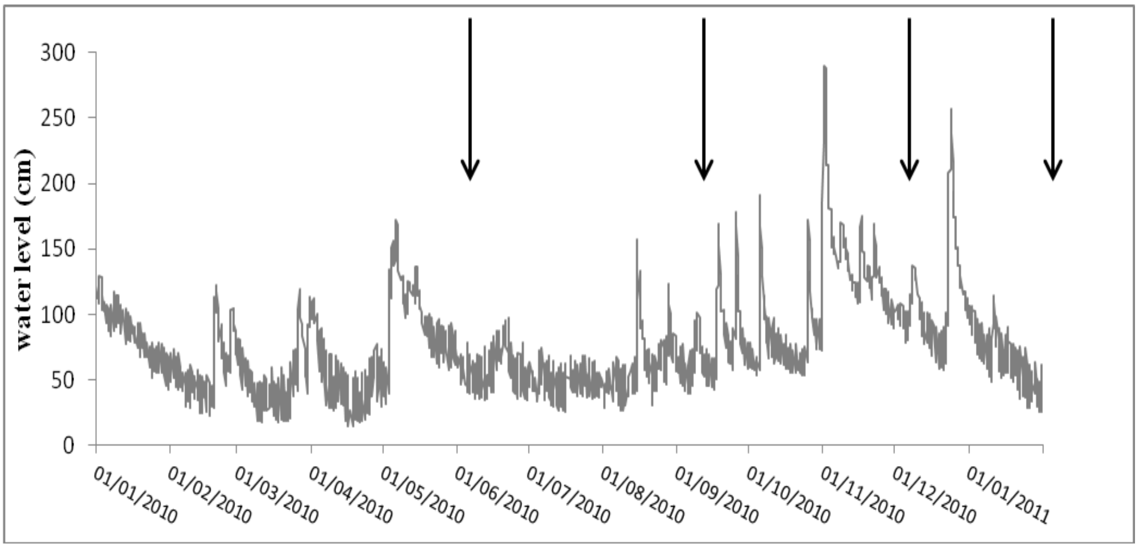


Figure 3.1 Water level of the Tagliamento recorded at the hydrometer of Villuzza (one kilometer downstream of the study area) from the 1st of January 2010 to the 31st of January 2011. Black arrows indicate the day the trapping of small mammals started in each trapping season (spring, summer, autumn, winter).

3.2.4 Spatial variables

Data on the spatial attributes of the islands were obtained through digital images and field measurements. ArcGis version 9.3 (Environmental Systems Research Insitute, Inc., Redlands, California, USA) Geographical Information System (GIS) tools were used to measure the following spatial variables of the islands: *area*, *distance from the mainland; distance to the nearest island; distance to the nearest largest island* and *proximity index within 270m of each island (PI270)*. The last variable, the proximity index (Gustafson and Parker 1994) quantifies the spatial context of a habitat patch in relation to its neighbours and to its size and distinguishes sparse distributions of small habitat patches from clusters of large patches. The proximity index was calculated within a buffer of 270 m from each island (edge to edge distance), because this distance represented the average distance travelled by mice in-between islands revealed by the capture-mark-recapture technique over the entire study period (average distance=270m±99, range: 70-425m, N =18).

To achieve a single variable that could represent the degree of isolation of each island, a PCA using all the variables describing isolation was performed (i.e. distance from the mainland, distance to the nearest island, distance to the nearest large island, PI270). The first component of the PCA strongly loaded on the PI270 of each island (99.6%) and created a gradient from large negative values for those islands which were far from the mainland but were surrounded by large islands (for example I7 in Figure 2.7, chapter 2, section 2.2), to large positive values for those islands which were closer to the riparian forest but were surrounded just by small islands (for example I14, I15 and I16). The first axis of this ordination explained 93% of the variation in the degree of isolation of each island, and therefore it was considered to effectively represent the relative level of island isolation. Given the high correlation between PC1 and PI270 (>99% correlation), PI270 was used as the single measure describing the degree of isolation of each island.

3.2.5 Statistical methods

Causal interaction between variables

Studying the effects of scale-dependent variables and their interactions on animal diversity requires a multivariate approach. To analyse the relationship between biotic, abiotic, spatial variables and small mammal diversity, Path Analysis was used. Path Analysis is a method for partitioning relationships amongst all the variables in consideration on the basis of hypothetical pathways of interaction that are identified *a priori* by the researcher on the basis of personal knowledge or literature reviews. The paths between the variables are expressed first in a path diagram and then in equation form, where the response variables are driven by one or more predictor variables. The response variables in one equation may form predictors in others, thereby forming sequences of causal relationships. In other words, Path Analysis simply tests how a well-postulated causal pathway that is built *a priori* fits the observed data in a modeling context.

Correlation analysis (Pearson correlation coefficient) was run between all the explanatory variables under investigation in order to explore the relations between them. The matrix of correlation obtained was subsequently used as input for running Path Analysis (Wright 1934), to investigate the causal relationships between the measured variables. Path Analysis tests whether the variables in the path are interrelated by examining the variances and covariances of the variables. Models are fitted by maximum likelihood. By comparing goodness of fit criteria (GFI) and Akaike Information Criteria (AIC) estimated for each model, it is possible to compare competing models for the underlying process and to identify the most parsimonious model for the available data (Fox 2002). This method has previously been used to investigate the relationship between patch scale and landscape scale variables on diversity of beetles in agricultural landscapes (Yaacobi et al. 2007) and is usually recommended for cases where the knowledge of the natural history of a system is sufficient to construct *a priori* path diagrams.

In this study, an *a priori model* was developed on the basis of the literature describing variables regulating small mammal distribution and community structure in a mainland-island system and the mechanisms of island formation on the Tagliamento floodplain. The *a priori* model was then compared with simpler models, which did not include pathways for which the association was shown to be non-significant. The extent to which the structure of the model differed from the *a priori* model was assessed using Chi-square. With Chi-square it is possible to test the difference between the observed data and the hypothesized *a priori* model. Because, hopefully, the hypothesized *a priori* model should fit the data, it would be important to find little or no difference between the observed data and the hypothesized model. This means that the observed covariance matrix is similar to the predicted covariance matrix, that is, the matrix predicted by the model. Therefore in order to retain a model, Chi-square has to be not significant. In this study the best pathway model (i.e. *the most parsimonious model*) was defined as that with the smallest AIC where all the interaction paths were significant (Fox 2002). The models were fitted in R using the sem library (Fox 2002).

Construction of the a priori model

Path diagrams contain two different types of variable: *manifest variables* and *residual error variables*. *Manifest variables* are directly observed and measured by the researcher and are divided into exogenous variables and endogenous variables. Exogenous variables are independent variables affecting a model without being affected by it. They are variables causing an effect and whose qualitative characteristics and method of generation are not specified by the model builder. Endogenous variables are variables whose values are determined by the pathways in the model (i.e. by other variables in the model). Endogenous variables are dependent variables that can be influenced by some variables and at the same time be the cause of other variables. *Residual error variables* represent all other un-modelled causes of variability. The residual error is an exogenous independent variable that is not directly measured and defines unspecified or unexplained causes. In a system like the riverine islands of the Tagliamento, landscape configuration, floods and availability of food for small mammals were considered to be important variables that could influence small mammal diversity. The *a priori* model assumed that there were two exogenous variables (area and island isolation), and three endogenous variables (floods, seed species diversity and small mammal diversity (Figure 3.2A).

In the *a priori* model it was assumed that the size of islands, represented by the variable area, would impact on small mammal diversity (Fox and Fox 2000). Given the direct relation between area and height of the islands on the gravel bars (Kollmann et al. 1999), larger islands are also likely to be flooded less frequently, and so the *a priori* model also took into account a relationship between the variable area and the variable floods. Kollmann et al. (1999) found that an increase in island area corresponds to an increase in island plant species diversity along this study reach of the Tagliamento. As plant species diversity is strongly correlated to seed species diversity (Spearman correlation coefficient: $\rho=0.84$, $p=0.00$) in the study area, due to the dominant vegetation being trees and shrubs that produce seeds, it was expected that the variable area was correlated to the variable seed species diversity. Consequently, it was hypothesized that a higher index of seed species diversity should result in an increase in the value of the variable small mammal diversity.

Other studies on small mammals found diversity of available food to be the proximate factor influencing diversity of forest small mammals (e.g. Miller and Getz 1977). It was also hypothesized that island isolation would directly impact on small mammal species diversity (MacArthur and Wilson 1967) with increasing isolation being responsible for lower values of small mammal diversity, due to the high risk for small mammals to experience predation travelling long distances on open habitats like gravel bars and also to the fact that re-colonisation is slower in islands that are far away from source habitats.

Finally it was assumed that any increase in the number of times an island had been flooded would impact on small mammal diversity. Previous studies have revealed that small mammals facing a flood not only run a high risk of drowning, but even if they reach non-flooded areas, mortality can still remain high, due to hypothermia, stress and exhaustion (Pachinger and Haferkorn 1998).

To satisfy the assumptions of normality for undergoing Path Analysis, a logarithmic transformation of all variables was applied before running the analysis. Logarithmic transformation was chosen because of the positive skewed distribution of some variables like area, seed species diversity, small mammal diversity and because, like in the Island Biogeography Theory (MacArthur and Wilson 1967), exponential relationships between some of the variables (i.e. area and small mammal diversity, isolation and small mammal diversity) were expected.

3.3 Results

3.3.1 Small mammal density and diversity

A total of 2188 trap nights was carried out resulting in a capture rate of 4.78 individuals/100 TN of *A. agrarius*, 11.0 individuals/100 TN of *A. sylvaticus* and 9.7 individuals/100 TN of *A. flavicollis*. Small mammal diversity ranged from 0.0 (for the islands where no species or just one species of small mammal were trapped) to 1.2 (Table 3.1).

Table 3.1 *A. flavicollis (Af)*, *A. agrarius (Ag)* and *A. sylvaticus (As)* annual population densities (Average number of individuals trapped on each island/100 TN), Index of Shannon for small mammal diversity(SM diversity) and mean value of seed species diversity (SS diversity) on each of the trapped islands (number in parenthesis indicate the number of 10 x 10m quadrants laid down on each island to estimate seed species diversity. Class size indicates whether the trapped island was small (S, ID in blue), medium (M, ID in black), or large (L, ID in red).

ID	***Class size***	***SS diversity***	***Af***	***Ag***	***As***	***SM diversity***
I2	S	0.0 ± 0.0 (1)	0.0 ± 0.0	0.0 ± 0.0	66.7 ± 40.8	0.0
I3	S	0.0 ± 0.0 (1)	0.0 ± 0.0	0.0 ± 0.0	33.3 ± 50.0	0.0
I15	S	0.5 ± 0.2 (2)	0.0 ± 0.0	0 ± 0.0	0.0 ± 0.0	0.0
I14	S	0.9 ± 0.3 (2)	33.3 ± 57.7	0 ± 0.0	0.0 ± 0.0	0.0
I4	S	0.0 ± 0.0 (1)	66.7 ± 115.5	0.0 ± 0.0	11.1 ± 16.7	0.4
I16	M	0.9 ± 0.3 (4)	0.0 ± 0.0	0 ± 0.0	0.0 ± 0.0	0.0
I11	M	0.0 ± 0.0 (2)	6.2 ± 12.5	0 ± 0.0	20.8 ± 17.5	0.5
I8	M	0.3 ± 0.3 (4)	7.8 ± 9.7	0.0 ± 0.0	29.4 ± 19.1	0.5
I17	M	0.8 ± 0.3 (4)	0.0 ± 0.0	0 ± 0.0	12.6 ± 13.1	0.6
I7	M	0.7 ± 0.5 (4)	2.3± 4.5	6.2 ± 12.5	22.3 ± 20.8	0.7
I13	M	1.9 ± 0.2 (2)	13.4 ± 15.5	10.3 ± 13.5	14.1 ± 17.6	1.1
I5	L	0.5 ± 0.4 (6)	8.0 ± 9.5	1.7 ± 3.3	111.0± 4.3	0.9
I12	L	1.0 ± 0.2 (8)	5.4 ± 6.3	1.0 ± 2.0	9.3 ± 6.9	1.0
I18	L	1.1 ± 0.3 (8)	1.8 ± 3.2	3.7 ± 3.2	7.4 ± 8.5	1.0
I10	L	0.9 ± 0.6 (4)	8.1 ± 9.9	5.0 ± 10.0	10.0 ± 10.7	1.1
I6	L	0.9 ± 0.6 (13)	12.2 ± 3.4	8.2 ± 8.6	6.6 ± 7.6	1.2
I9	L	1.3 ± 0.3 (8)	6.8 ± 4.8	8.4 ± 2.2	8.5 ± 6.2	1.2

3.3.2 Effects of patch scale and landscape scale variables on small mammal diversity

Seven explanatory variables and one dependent variable (small mammal diversity) were considered in this analysis. Their ranges and mean values shown in Table 3.2.

Table 3.2 Names of the measured variables, their measured ranges and mean values (with SD). 'Scale' indicates whether the variable acts at patch (i.e. island) scale or at landscape scale.

Variable name	***range***	***mean value* ± SD**	***scale***
area (ha)	0.0-4.2	0.9±1.0	patch
distance from mainland (m)	10.8-310.6	139.5±94.5	landscape
distance nearest island (m)	9.2-144.7	46.2±6.4	landscape
distance nearest large island (m)	9.2-1032.0	203.0±261.0	landscape
proximity index 270	53.0-4033.7	731.3±968.1	landscape
floods (number of per island)	0.0-4.0	2.1±1.1	landscape
seed species diversity	0.0-1.9	0.6±0.5	patch
small mammal diversity	0.0-1.2	0.6±0.5	patch

Correlation between the input variables

Area of islands was positively correlated with seed species diversity, isolation and with small mammal diversity, the first two correlations not being significant. Seed species diversity was found to be significantly positively correlated solely with small mammal diversity (Table 3.3), while the correlations with all the other variables were not significant. Isolation and floods were the two variables acting at the landscape scale. Only floods were significantly correlated with small mammal diversity: the higher the number of times an island was flooded, the lower the small mammal diversity (Table 3.3).

Table 3.3 Pearson correlations coefficients between input variables. Significant correlations at p≤0.05 level are highlighted in bold. N=17.SM Diversity=small mammal diversity; SS diversity=seed species diversity.

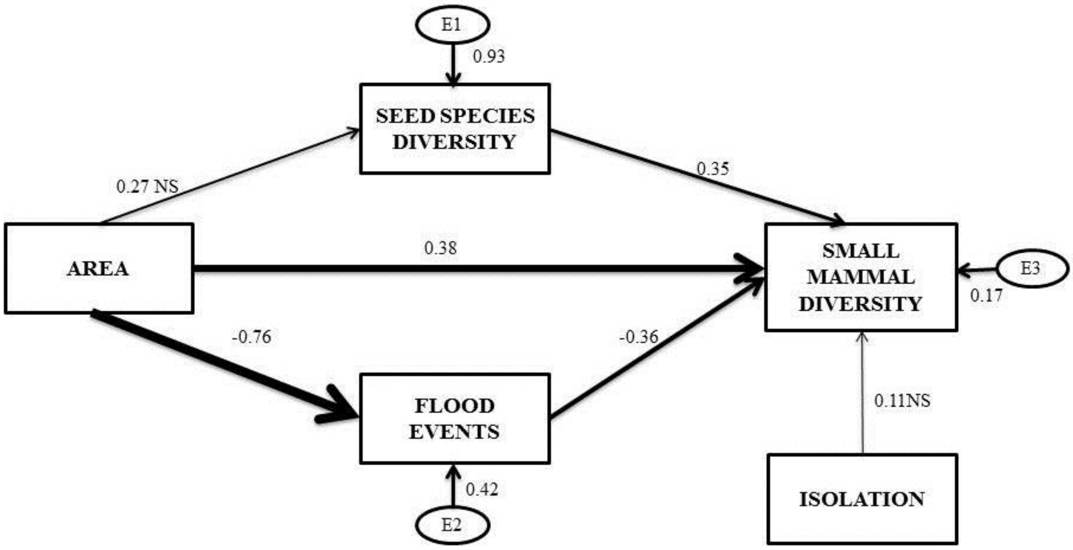
	SS diversity	*isolation*	*floods*	*SM diversity*
area	0.27	0.17	**-0.76**	**0.77**
SS diversity		0.01	-0.40	**0.60**
isolation			-0.24	0.27
floods				**-0.86**

3.3.3 Causal interactions between variables

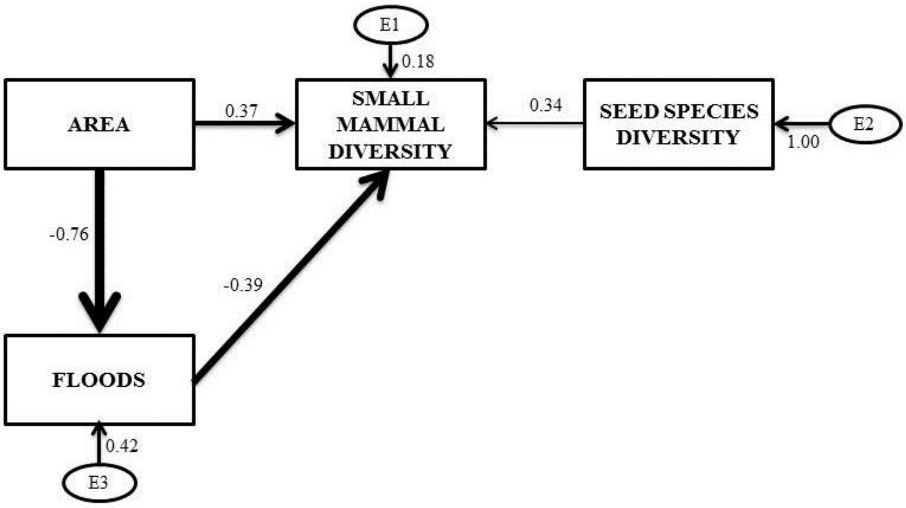
Causal relationships between variables were investigated through Path Analysis. Standardized coefficients on each pathway and results of the Chi-square test for the *a priori* model are shown in Figure 3.2A; the parameter estimates for the model are given in Table 3.4. The *a priori* model resulted in a non-significant value of Chi-square (Chi square=2.27, p=0.52), and the GFI value was acceptable (0.95) (Byrne 1994). In this model (AIC=20.27), the pathway between small mammal diversity and isolation was not significant. Therefore the variable isolation was removed for the evaluation of the most parsimonious model, leaving just one exogenous variable: area. Likewise, the path between area and seed species diversity was not significant, so it was removed.

The *most parsimonious model* (AIC=16.84), included the exogenous variable area and three other endogenous variables: small mammal diversity, floods and seed species diversity. Area had a direct positive effect on small mammal diversity and a direct negative effect on floods (i.e. large and medium islands were flooded fewer times than small islands). Moreover, area had an indirect effect on small mammal diversity through a path connecting it with the variable floods, which in turn negatively affected small mammal diversity. This model resulted in a not significant

Chi-square and gave a GFI comparable to the GFI obtained for the *a priori* model, so it was considered acceptable (Byrne 1994). Furthermore the lower value for the AIC obtained for the *most parsimonious model* indicates that it fitted the data better than the *a priori model* (Figure 3.2B). For the *most parsimonious model* the contribution of the exogenous variable area to small mammal diversity was: 0.37+ ((-0.76)*(-0.39))] = 0.67.



A. a priori model
Chi-square=2.27, df=3, p=0.52, GFI=0.95, AIC=20.27



B. Parsimonious model
Chi-square = 2.84, df=2, p=0.24, GFI=0.96, AIC=16.84

Figure 3.2 Models used in Path Analysis and summaries of the Path Analysis results. Standardised path coefficients are reported close to the arrows indicating the relations between variables. Variables identified with E, indicate residual errors for the endogenous variables. The thicker the arrow, the higher the value of the path coefficient found. GFI = Goodness of Fit Criteria, AIC= Akaike Information Criteria, NS=non-significant pathway.

Table 3.4 Parameter estimates for the pathways of the *a priori model*. Significant pathways at p≤0.05 level are highlighted in bold. z = z value. SE=standard error.

Relationship	***Estimate***	***SE***	***z***	***p***
area - seed species diversity	0.27	0.24	1.12	0.26
seed species diversity- small mammal diversity	0.35	0.11	3.29	0.00
area - small mammal diversity	0.38	0.16	2.35	0.02
isolation - small mammal diversity	0.11	0.10	1.10	0.27
floods - small mammal diversity	-0.36	0.16	-2.31	0.02
area - floods	-0.76	0.16	-4.67	0.00
seed species diversity	0.93	0.33	2.82	0.00
small mammal diversity	0.17	0.06	2.82	0.00
floods	0.42	0.15	2.82	0.00

Table 3.5 Parameter estimates for pathways of the most *parsimonious model*. All of the pathways were found to be significant at p≤0.05 level. z = z value. SE = standard error.

3.4 Discussion

Relationship	***Estimate***	***SE***	***z***	***p***
seed species diversity- small mammal diversity	0.34	0.11	3.19	0.00
area - small mammal diversity	0.37	0.16	2.29	0.02
floods - small mammal diversity	-0.39	0.16	-2.44	0.01
area - floods	-0.76	0.16	-4.67	0.00
seed species diversity	1.00	0.35	2.82	0.00
small mammal diversity	0.18	0.06	2.82	0.00
floods	0.42	0.15	2.82	0.00

This study is the first to use a landscape ecology approach for analysing variables regulating the species diversity of small mammals in riparian habitats at a relatively broad scale. Unlike previous research, describing the composition of small mammal communities in riparian habitats (e.g. Romanowski et al. 2008; Wijnhoven et al. 2005), or examining the role of key fine scale habitat features, such as log distribution, in regulating these communities (e.g. Churchfield 1998; Osbourne et al. 2005), the role of variables acting at broader scales in influencing patterns of small mammal diversity was investigated. Results suggest that small mammal species diversity in heterogeneous riparian landscapes, are regulated by variables working both at patch and landscape scales.

3.4.1 Small mammal responses to patch scale variables

Two variables acting at patch scale were significantly correlated to small mammal diversity on the Tagliamento river islands, namely island area and seed species diversity (Table 3.3). Values of small mammal diversity appeared to significantly increase with island area, as predicted by fundamental tenets of island biogeography theory (MacArthur and Wilson 1967) and as reported in landscape ecology studies where the theory was applied to mammals, including small mammals (Adler and Wilson 1985; Fox and Fox 2000; Hanski and Kuitunen 1986; Lomolino 1984). The relation between island area and species diversity is often explained through the causal sequence (MacArthur and Wilson 1967):

Small island size → reduced habitat variety → reduced equilibrial number of species

This sequence explains how a reduction in the size of the islands implies a reduction in their habitat diversity and therefore causes a decrease in the number of coexisting species.

This study revealed that there was a positive relationship between area and seed species diversity for the islands of the Tagliamento. Larger islands were generally characterized by higher values of seed species diversity (Table 3.1 and results of chapter 4, section 4.3.2 and Figure 4.6), due to the higher plant species diversity that characterizes large islands compared to small ones on the Tagliamento floodplain (Kollman et al. 1999). It is likely that plant species diversity (and therefore seed species diversity) reflects heterogeneity of plant functional groups (Power 1972), and therefore promotes habitat variety, as discussed by MacArthur and Wilson (1967), such that more small mammal species can coexist on the basis of resource partitioning and microhabitat differentiation (Fox and Fox 2000). It can be therefore concluded that on the Tagliamento floodplain, large islands, being characterized by a higher seed species diversity would more likely allow the three species of *Apodemus* to coexist, while small islands, which tend to be characterized by less plant variety (especially less shrub species) and less cover, would increase competition between species and would be characterized by a lower small mammal diversity.

Medium islands I7 and I13 were an exception: they showed the co-occurrence of all three species of *Apodemus* and they were also characterized by medium-high values of seed species diversity (Table 3.1). These particular islands were therefore more similar in their animal and vegetation community to large islands. This could have happened because: (1) they are remnants of larger and more serially-advanced islands that have been reduced in size in the last six years due to fluvial disturbance (in the case of I13) or (2) because, like I7, they are very close to a large island where small mammal diversity reached the highest values (I6), therefore potentially making easy for individuals of different species the movement in-between islands and consequently increasing their number of species (distance I6-I7=20m).

When looking at individual patterns of distribution of each species on islands, trends supported by the literature emerge, especially for *A. flavicollis* and *A. sylvaticus*. *A. flavicollis* is a species strongly dependent on the forest environment (Montgomery 1985), so medium and large islands (where the species was captured more frequently, i.e. in 10 out of 12 cases) might provide them with the dense vegetation cover they require. On the other hand, *A. sylvaticus* prefers forest edges and bushes and therefore it is a species typical of forest and open habitat mosaic (Geuse et al. 1985). *A. sylvaticus* reached the highest annual densities on very small islands (I2, I3, I7, I8, I11), which are generally characterized by a high cover of *Salix* spp. and by relatively high values of 'edge' habitat. On large islands, with the exception of I6 (the largest island), this species was always the most abundant one, suggesting that the habitat mosaic of the Tagliamento floodplain represent a suitable habitat for *A. sylvaticus*, which tends to be a generalist in terms of its habitat preferences (Diaz et al. 1998). In contrast, *A. agrarius* is not a species permanently dependent on the forest environment (Amori et al. 2008). Usually, during the crop vegetation period (spring to autumn) this species is mainly found in agricultural fields, from where it enters forests in search of hiding places. In autumn, individuals move to the forest where they spend the winter. The general low capture rates obtained for *A. agrarius* on islands (which was confined just to large islands and to I7 and I13, Table 3.1), could be a consequence both of the low suitability of the mosaic of the Tagliamento floodplain for the species, or of competition by the other two species (Gliwicz 1981; Ylonen et al. 1991) (see chapter 4 for further results of an analysis of their life histories at the study area).

3.4.2 Small mammal responses to landscape scale variables

The fact that small mammal diversity on islands did not show a significant decreasing trend with increasing isolation of the islands might be due to several reasons.

First, the average distance between the mainland and the trapped islands (139.5m±94.5) was far lower than the values of maximum dispersal distances recorded for the three species trapped (Kozakiewicz et al. 1999; Liro and Szacki 1987; Stradiotto et al. 2009); secondly, it was also lower than the average inter-island movement revealed by trapping in the present thesis (i.e. 270 m). Moreover, islands were characterized by high values of proximity and none of the islands were found to have an empty 'neighborhood' at 270m, i.e. all the islands where surrounded by other islands within a distance of 270m, and in 12 out of 17 cases these other islands were represented by at least one large island (where the values of small mammal diversity were the highest). Therefore, it is likely that each of the studied islands could easily be colonized by small mammals and each large island could provide a source of animals for the smaller ones, following meta-population dynamics and the rescue effect (Levins 1969). As a result, other mechanisms, rather than isolation, are more likely to be influential on small mammal diversity of the islands at the landscape scale, in the studied area. Indeed, Path Analysis identified floods as an important variable influencing small mammal diversity.

The number of times an island was flooded strongly negatively influenced small mammal diversity. No other study has examined the effect of floods on species diversity in natural or semi-natural riparian habitats subject to periodical flooding, but Hanley and Barnard (1999) found that other variables, such as small mammal abundance, could be strongly influenced by floods.

Andersen et al. (2000) noted that small mammals facing a flood commonly tend to remain in the original home range until ‘forced’ to leave. They noticed also that non-arboreal species perceive floods like a catastrophe, succumbing, while species capable of using an arboreal refuge face a more variable risk, determined in part by timing and duration of the flood. Moreover, Wijnhoven et al. (2005) found that re-colonisation after a flood can be a very slow process which depends on the mobility of the species, on the number of re-colonisation sources and the number of survivors from which a population may recover.

From data presented in this chapter, it appears that floods have a significant impact on small mammal populations. The two big floods of early November and late December (Figure 3.1) could have affected the autumn and winter densities of small mammals and consequently the values of small mammal diversity. Indeed, the lower island seasonal densities for the *Apodemus* species observed in autumn and winter in respect to the spring and summer values on several islands (see Chapter 4, Appendix 4.1), by affecting the value of annual seasonal density, would have made the values of the index of small mammal diversity on islands to decrease.

If we consider an index that takes into account changes in the values of island seasonal density in-between seasons (not including islands where population density was zero in the following seasons) and use the mainland as control (where no flooding happened and therefore trends in population densities reflect true population dynamics of the three species), it appears that mostly the species tend to be affected by floods as follows:

-Between summer and autumn (when the big flood of November happened), *A. flavicollis* and *A. agrarius* densities decreased in more than the 50% of the islands, while *A. sylvaticus* densities decreased only on one island. On the non-flooded mainland, a reduction in density between summer and autumn occurred for *A. flavicollis* and *A. sylvaticus* at one out of three samples sites while *A. agrarius* density decreased in all the sampled sites.

-Between autumn and winter (when the big flood of December happened), *A. flavicollis* and *A. agrarius* showed a reduction in density in 75% and 33% of the islands respectively, while for *A. sylvaticus* this reduction happened in less than 50% of the islands. On the mainland, between autumn and winter *A. flavicollis* and *A. agrarius* density decreased in 100% of mainland trapping sites, while for *A. sylvaticus* density remained stable or increased (see Chapter 4, Appendix 4.1 for the indexes seasonal densities of the three species).

These trends suggest that the big floods of November and December might have been the cause of the decreasing densities of *A. flavicollis* and of *A. sylvaticus* on islands, given that their densities remained relatively stable on the non-flooded mainland respectively between summer and autumn (for both species) and between autumn and winter (for *A. sylvaticus*). As for *A. agrarius* the changes in densities between summer and autumn are comparable in the two habitats as well as changes between autumn and winter. So, other ecological mechanism or micro-habitat specialisation rather than floods might have affected the trend for decreasing densities for *A. agrarius,* though these were quite low on islands regardless.

A. sylvaticus and *A. flavicollis* are good climbers and beside burrows, they also frequently use ground and above-ground nests (Sarà 2008; Stepankova and Vohralik 2009). *A. agrarius* is more subterranean and fossorial than the other two species, showing a burrowing mode of life (Kuncova and Frynta 2009). In the previous section it was discussed how the low densities of *A. agrarius* in the whole study area could have been the results of (1) the lack of favourable environmental conditions for the species and/or (2) mechanisms of interspecific competition with the other two *Apodemus* species. It is also likely that, the low densities of *A. agrarius* on islands could have been due to (3) its higher risk of drowning following island inundation, given its burrowing mode of life. However, all these three argumentations would contribute to create fewer re-colonisation sources and survivors to re-found new populations and suggests islands could be re-colonised more easily by the other two species, which showed in general higher seasonal densities and climbing skills. These conclusions are sustained by previous studies which revealed that in an *Apodemus* community, high local densities of a particular species result in higher number of dispersers colonizing different habitats (Montgomery and Gurnell 1985).

3.4.3 The combined effect of patch and landscape scale analysis

The use of Path Analysis enabled an identification of the most important pathways determining species diversity patterns across the active tract of the River Tagliamento. This analysis revealed that there was an interaction between variables acting at the patch scale and variables acting at the landscape scale in regulating the small mammal diversity of islands. In this study the *most parsimonious model* described small mammal diversity on river islands being regulated by the concurrent action of area of the islands, seed species diversity (patch scale variables) and disturbance in the form of floods (landscape scale variable).

These variables interact in a particular way within the context of the Tagliamento floodplain. The *most parsimonious model* produced a negative path between area and floods, i.e. the larger the islands, the lower the number of times they were inundated. This result would be in accordance with previous findings on the Tagliamento. Larger islands are generally also older islands and often have relatively high elevations on top of the gravel bars (up to 2-3 m, due to repeated episodes of sediment deposition) (Kollman et al. 1999). It is likely that being higher on the gravel bar, older islands could better resist a flood and therefore they might be less ‘disturbed’ by these stochastic events. Being less disturbed, larger (i.e. older) islands could sustain larger communities of small mammals. On the Tagliamento, stochastic disturbance (i.e. a flood) can either completely destroy a river island and reset the vegetation cover to zero, or can cause the partial erosion of their vegetation structure impacting on plant species composition and degree of ground cover (Gurnell et al. 2001). For mammals, vegetation provides shelter, food and nesting opportunities, as well as protection from predators and antagonistic conspecific and heterospecific encounters (Birney et al. 1976; Parmenter and MacMahon 1983). Loss of vegetative cover following a stochastic event (like a flood) has been shown to modify animal community structure in direct relation to species-specific cover requirements and species with strict cover requirements may be disadvantaged in comparison with species with less strict needs (Fox 1982; Monamy and Fox 2000).

Relationships between area, mammal species diversity and disturbance have been explored by Dunstan and Fox (1996) and by Fox and Fox (2000) for remnant forest fragments. They found that degree of disturbance had a significant impact on species richness and noted that increased levels of disturbance (i.e. disturbance by people, by livestock or even stochastich disturbance) produced a relatively greater decrease in the number of species on smaller habitat islands than on larger habitat islands.

This work has therefore revealed that, studying the interaction between landscape scale and patch scale variables is important for the understanding the diversity of small mammal communities also in natural and semi-natural riverine landscapes. The natural dynamism of the Tagliamento promotes high habitat heterogeneity in the floodplain, which in turn affects mammal species composition and diversity. Any possible management plans or actions which would alter the natural heterogeneity and the dynamic nature of the riverine mosaic of the Tagliamento, should take into account the findings of this study.

3.5 References

Adler, G.H. and Wilson, M.L., 1985. Small mammals on Massachusetts islands: the use of probability functions in clarifying biogeographic relationships. Oecologia 66, 178-186.

Amori, G., Contoli, L., Nappi, A., 2008. Mammalia II- Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia. Calderini, Milano.

Andersen, D.C., Wilson, K.R., Miller, M.S., Falck, M., 2000. Movement patterns of riparian small mammals during predictable floodplain inundation. Journal of Mammalogy 81, 1087-1099.

Birney, E.C., Grant, W.E., Baird, D.D., 1976. Importance of Vegetative Cover to Cycles of Microtus Populations. Ecology 57, 1043-1051.

Bolger, D.T., Alberts, A.C., Sauvajot, R.M., Potenza, P., McCalvin, C., Tran, D., Mazzoni, S., Soula M.E., 1997. Response of rodents to habitat fragmentation in coastal southern California. Ecological Applications 7, 552-563.

Bowers, M., Gregario, K., Brame, C.J., Matter, S.F., Dooley, J.L., 1996. Use of space and habitats by meadow voles at the home-range, patch and landscape scales. Oecologia 105, 107-115.

Bowers, M.A. and Dooley, J.L., 1991. Role of habitat mosaics on the outcome of two-species competition. Oikos 60, 180-186.

Bowman, J., Forbes, G., Dilworth, T., 2001. Landscape context and small-mammal abundance in a managed forest. Forest Ecology and Management 140, 249-255.

Byrne, B.M., 1994. Structural equation modeling with EQS and EQS/Windows. Sage, Thousand Oaks, CA.

Capizzi, D. and Filippucci, M.G., 2008. Apodemus flavicollis, In Fauna d'Italia. Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia. eds G. Amori, L. Contoli, A. Nappi. Calderini, Milano.

Churchfield, S., 1998. Habitat use by water shrews, the smallest of amphibious mammals, In Behaviour and ecology of riparian mammals. eds N. Dunstone, M. Gorman, p. 391. Cambridge University Press, Cambridge.

Cockburn, A. and Lidicker , W.Z., 1983. Microhabitat heterogeneity and population ecology of a herbivorous rodent, Microtus californicus. Oecologia 59, 167-177.

Collins, R.J. and Barrett, G.W., 1997. Effects of habitat fragmentation on meadow vole (Microtus pennsylvanicus) population dynamics in experimental landscape patches. Landscape Ecology 12, 63-76.

Diaz, M., Santos, T., Telleria, J.L., 1998. Effects of forest fragmentation on the winter body condition and population parameters of an habitat generalist, the wood mouse Apodemus sylvaticus: a test of hypohtesis. Acta Oecologica 20, 39-49.

Diffendorfer, J.E., Gaines, M.S., Holt, R.D., 1995. Habitat fragmentation and movement of three small mammals (Sigmodon, Mcrotus and Peromyscus). Ecology 76, 827-839.

Diffendorfer, J.E., Gaines, M.S., Holt, R.D., 1999. Patterns and impacts of movement at different scales in small mammals, In Landscape ecology of small mammals. eds G.W. Barret, J.D. Peles, p. 347. Springer.

Dunstan, C.E. and Fox, B.J., 1996. The effects of fragmentation of rainforest on ground-dwelling small mammals on the Robertson Plateau, New South Wales, Australia. Journal of Biogeography 23, 187-201.

Eccard, J.A., Walther, R.B., Milton, S.J., 2000. How livestock grazing affects vegetation structures and small mammals distribution in the semi-arid Karoo. Journal of Arid Environments 46, 103-106.

Fitzgibbon, C.D., 1997. Small mammals in farm woodlands: The effects of habitat, isolation and surrounding land-use patterns. Journal of Applied Ecology 34, 530-539.

Forman, R.T.T. and Godron, M., 1981. Patches and structural components for a landscape ecology. BioScience 31, 733-740.

Fox, B.J., 1982. Fire and mammalian secondary succession in Australian coastal heath. Ecology 63, 1332-1341.

Fox, B.J. and Fox, M.D., 2000. Factors Determining Mammal Species Richness on Habitat Islands and Isolates: Habitat Diversity, Disturbance, Species Interactions and Guild Assembly Rules. Global Ecology and Biogeography 9, 19-37.

Fox, J., 2002. An R and S-PLUS Companion to Applied regression. Sage, Thousand Oaks, CA.

Frey, J.K., Bogan, M.A., Yates, T.L., 2007. Mountaintop island age determines species richness of boreal mammals in the American Southwest. Ecography 30, 231-240.

Gascon, C., Lovejoy, T.E., Bierregaard Jr, R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S., 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation 91, 223-229.

Geuse, P., Bauchau, V., Le Boulenge, E., 1985. Distribution and population dynamics of bank voles an wood mice in a patchy woodland habitat in central Belgium. Acta Zoologica Fennica 173, 65-68.

Gliwicz, J., 1981. Competitive interactions within a forest rodent community in central Poland. Oikos 37, 353-362.

Gurnell, A.M., Petts, G.E., Hannah, D.M., Smith, B.P.G., Edwards, P.J., Kollmann, J., Ward, J.V., Tockner, K., 2001. Riparian vegetation and island formation along the gravel-bed fiume Tagliamento, Italy. Earth Surface Processes and Landforms 26, 31-62.

Gurnell, A., Tockner, K., Edwards, P., 2005. Effects of deposited wood in biocomplexy of river corridors. Frontiers in Ecology and Environment 3, 377-382.

Gurnell, J. and Flowerdew, J.R., 2006. Live trapping small mammals. A practical guide, 4^{th} edition Mammal Society, London, UK.

Gustafson, E.J. and Parker, G.R., 1994. Using an index of habitat patch proximity for landscape design. Landscape and Urban Planning 29, 117-130.

Hanley, T.A. and Barnard, J.C., 1999. Spatial Variation in Population Dynamics of Sitka Mice in Floodplain Forests. Journal of Mammalogy 80, 866-879.

Hanski, I., 1986. Population dynamics of shrews on small islands accord with the equilibrium model. Biological Journal of the Linnean Society 28, 23-36.

Hanski, I. and Kuitunen, J., 1986. Shrews on small islands: epigenetic variation elucidates population stability. Holarctic Ecology 9, 193-204.

Holland, G.J. and Bennett, A.F., 2007. Occurrence of small mammals in a fragmented landscape: The role of vegetation heterogeneity. Wildlife Research 34, 387-397.

Kent, M. and Coker, P., 1992. Vegetation description and analysis: a practical approach. CRC press, Boca Raton, Florida.

Kollmann, J., Vieli, M., Edwards, P.J., Tockner, K., Ward, J.V., 1999. Interaction between vegetation development and island formation in the Alpine river Tagliamento. Applied Vegetation Science, 25-36.

Kozakiewicz, M., Gortat, T., Kozakiewicz, A., Barkowska, M., 1999. Effects of habitat fragmentation on four rodent species in a Polish farm landscape. Landscape Ecology 14, 391-400.

Kuncova, P. and Frynta, D., 2009. Interspecific morphometric variation in the postcranial skeleton in the genus *Apodemus*. Belgian Journal Zoology 139, 133-146.

Kupfer, J.A., Malason, G.P., Franklin, S.B., 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. Global Ecology and Biogeography 15, 8-20.

Levins, R., 1969. Some demographic and genetic consequences of environmetal heterogeneity for biological control. Bulletin of the Entomological Society of America 15, 237-240.

Liro, A. and Szacki, J., 1987. Movements of the field mice Apodemus agrarius (Pallas) in a suburban mosaic of habitats. Oecologia 74, 438-440.

Lomolino, M.V., 1984. Mammalian island biogeography: effects of area, isolation and vagility. Oecologia 61, 376-382.

MacArthur, R.H. and Wilson, E.O., 1967. The Theory of Island biogeography. Princeton University Press.

Malard, F., Tockner, K., Dole-Olivier, M.J., Ward, J.V., 2002. A landscape perspective of surface - subsurface hydrological exchanges in river corridors. Freshwater Biology 47, 621-640.

McShea, W.J., Pagels, J., Orrock, J., Harper, E., Koy, K., 2003. Mesic Deciduous Forest as Patches of Small-Mammal Richness within an Appalachian Mountain Forest. Journal of Mammalogy 84, 627-643.

Michaux, J.R., Kinet, S., Filippucci, M.G., Libois, R., Besnard, A., Catzeflis, F., 2001. Molecular identification of three sympatric species of wood mice (Apodemus sylvaticus, A. flavicollis, A. alpicola) in western Europe (Muridae: Rodentia). Molecular Ecology Notes 1, 260-263.

Miller, D.H. and Getz, L.L., 1977. Factors influencing local distribution and species diversity of forest mammals in New England. Canadian Journal of Zoology 55, 806-814.

Monamy, V., and Fox, B.J., 2000. Small mammal succession is determined by vegetation density rather than time elapsed since disturbance. Austral Ecology 25, 580-587.

Montgomery, W.I., 1985. Interspecific competition and the comparative ecology of two congeneric species of mice, In Case Studies in Population Biology. ed. L.M. Cook, pp. 126-187. Manchester University Press, Manchester.

Montgomery, W.I. and Gurnell, A., 1985. The behaviour of Apdemus. Symposia of the Zoological Society of London 55, 89-115.

Mortelliti, A., Amori, G., Annesi, F., Boitani, L., 2009. Testing for the relative contribution of patch neighborhood, patch internal structure, and presence of predators and competitor species in determining distribution patterns of rodents in a fragmented landscape. Canadian Journal of Zoology 87, 662-670.

Nupp, T.E., Swihart, R.E., 2000. Landscape-level correlates of small-mammal assemblage in forest fragments of farmland. Journal of Mammalogy 81, 512-526.

Osbourne, J.D., Anderson, J.T., Spurgeon, A.B., 2005. Effects of habitat on small-mammal diversity and abundance in West Virginia. Wildlife Society Bulletin 33, 814-822.

Pachinger, K. and Haferkorn, J., 1998. Comparisons of the small mammal communities in floodplain forests at the Danube and Elbe rivers. Ekologia Bratislava 17, 11-19.

Pardini, R., Marques de Souza,S., Braga-Neto, R., Metzger,J.P., 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. Biological Conservation 124, 253-266.

Parmenter, R.R. and MacMahon, J.A., 1983. Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: the role of shrubs. Oecologia 59, 145-156.

Peltonen, A., Peltonen, S., Vilpas, P., Beloff, A., 1989. Distributional ecology of shrews in three archipelagoes in Finland. Annales Zoologici Fennici 26, 381-387.

Power, D.M., 1972. Number of bird species on the California islands. Evolution 26, 451-463.

Robinson, C.T., Tockner, K., Ward, J.V., 2002. The fauna of dynamic riverine landscapes. Freshwater Biology 47, 661-677.

Romanowski, J., Dudek, D., Kowalczyk, K., 2008. The role of islands in mantaining the connectivity of habitat for mammals in middle Vistula river valley. Ecohydrology & Hydrobiology 8, 411-418.

Sarà, M., 2008. The use of artificial nest-boxes by Apodemus sylvaticus dichrurus in Sicily. Folia Zoologica 57, 294-299.

Scott, D.M., Joyce, C.B., Burnside, N., 2008. The influence of habitat and landscape on small mammals in Estonian coastal wetlands. Estonian Journal of Ecology 57, 279-295.

Sher, A.A., Marshall, D.L., Gilbert, S.A:, 2000. Competition between native *Populus deltoids* and invasive *Tamarix ramosissima* and the implications for re-establishing flooding disturbance. Conservation Biology 14, 1744-1754.

Stepankova, J. and Vohralik, V., 2009. Vertical activity of the yellow-necked mouse (Rodentia: Muridae) at edge of a mixed forest. Folia Zoologica 58, 26-35.

Stradiotto, A., Cagnacci, F., Delahay, R., Tioli, S., Nieder, L., Rizzoli, A., 2009. Spatial organization of the yellow-necked mouse: Effects of density and resource availability. Journal of Mammalogy 90, 704-714.

Tattersall, F.H., Macdonald, D.W., Hart, B.J., Manly, W.J., Feber, R.E., 2001. Habitat use by wood mouse (Apodemus sylvaticus) in a changeable arable landscape. Journal of Zoology (London) 255, 487-494.

R Developmental Team, 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Tockner, K., Malard, F., Ward, V., 2000. An extension of the Flood Pulse Concept. Hydrological Processes 14, 2861-2883.

Tockner, K., Ward, J.V., Arscott, D.B., Edwards, P.J., Kollmann, J., Gurnell, A.M., Petts, G.E., Maiolini, B., 2003. The Tagliamento River: A model ecosystem of European importance. Aquatic Science 65, 239-253.

Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Ann. Rev. Ecol. Syst. 20, 171-197.

Van Apeldoorn, R.C., Oostenbrink, W.T., Van Winden, A., Van Der Zee, F.F., 1992. Effects of habitat fragmentation on the bank vole, Clethrionomys glareolus, in an agricultural landscape. Oikos 65, 265-274.

Ward, J.V., 1998. Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. Biological Conservation 83, 269-278.

Ward, J.V., Malard, F., Tockner, K., 2002. Landscape ecology: a framework for integrating pattern and processes in river corridors. Landscape Ecology 17, 35-45.

Wiens, J.A., 2002. Riverine landscapes: taking landscape ecology into the water. Freshwater Biology 47, 501-515.

Wijnhoven, S., Van Der Velde, G., Leuven, R.S.E.W., Smits, A.J.M., 2005. Flooding ecology of voles, mice and shrews: The importance of geomorphological and vegetational heterogeneity in river floodplains. Acta Theriologica 50, 453-472.

Wright, S., 1934. The method of path coefficients. Annals Mathematical Stat 5, 161-215.

Yaacobi, G., Ziv, Y., Rosenzweig, M.L., 2007. Effects of interactive scale dependent variables on beetle diversity patterns in a semi-arid agricultural landscape. Landscape Ecology 22, 687-703.

Ylonen, H., Altner, H.J., Stubbe, M., 1991. Seasonal dynamics of small mammals in an isolated woodlot and its agricultural surroundings. Annales Zoologici Fennici 28, 7-14.

Chapter 4 - The island syndrome of a rodent riparian community

Abstract

Early research on insular species focused greatly on the phenotypical peculiarities of island populations with respect to mainland populations and revealed that within mammals, insular rodents had the tendency to increase in body size on islands, while ungulates and carnivores often decreased in body size. Later studies revealed there are also several other demographic and behavioural patterns that have become apparent in island populations (e.g. changes in density, in the reproductive output and in the proportion of juveniles:adults in the population, etc): these differences are collectively termed the '*island syndrome*'.

In this chapter, the demographic and phenotypic expectations of the island syndrome are tested on populations of three species of *Apodemus* living on the river islands and riparian forest of the River Tagliamento: *A. flavicollis, A. agrarius* and *A. sylvaticus.*

Results showed that *A. sylvaticus* manifested some of the demographic traits of the island syndrome, with an increased density and an increased adult versus juveniles proportion on islands in respect to the mainland. On the contrary, *A. flavicollis* and *A. agrarius* revealed a decreased density, a decreased reproductive output and an increased juveniles versus adult proportion on islands. None of the three species showed changes in body size, besides a trend for a lower weight on islands. The mechanism which more likely explains the island syndrome traits found in *A. sylvaticus* is *density compensation*, which attributes an increased density of a species on islands to the fact that islands often only have a subset of the faunal community in comparison to the mainland.

The findings of this study indicate that some traits of the island syndrome, like an increased density and an increased adult proportion on islands can be manifested also in ephemeral islands, even after very short time since their isolation, but just in those species which have permanent populations on islands, like *A. sylvaticus* on the river islands of the Tagliamento. Moreover, this study highlights how island populations which are not permanently isolated from the mainland and whose dynamics are often disturbed by stochastic events like floods, do not show island syndrome traits like a modified body size: such modification of the phenotype would probably require more time or conditions where island isolation is permanent and time since isolation is longer.

4.1 Introduction

Early research on insular species focused greatly on the phenotypical peculiarities of island populations with respect to their mainland counter forms (e.g. Heaney 1978; Reyment 1983). One of the main patterns to emerge from these studies was a tendency amongst island races to exhibit a change in body size in comparison to mainland conspecifics. This trend was first described in mammals by Foster (1964), who noted that insular rodents had the tendency to increase in body size on islands, while ungulates and carnivores often decreased in body size. The theory was later extended by Van Valen (1973) and others (e.g. Lomolino 1985) to describe a tendency towards dwarfism on islands for large mammals and a tendency towards gigantism for small mammals. This phenomenon became the so-called '*island rule'*. Although much less well studied than dwarfism and gigantism, there are several other demographic and behavioural patterns that have become apparent in island populations. Adler and Levins (1994) termed these differences collectively the '*island syndrome*'.

Other demographic characteristics that differentiate island populations of small mammals from those on the mainland include: 1. higher population densities; 2. a higher proportion of adults to juveniles; and 3. lower reproductive output. For rodents, the island syndrome predicts that traits such as body size and density are expected to increase, whereas rates of reproduction and population cycles are expected to decrease (Adler and Levins 1994).

In this chapter, demographic and phenotypic expectations of the island syndrome are tested on the populations of the three species of *Apodemus* living on the river islands and riparian forest of the River Tagliamento*: A. flavicollis*, *A. agrarius* and *A. sylvaticus*.

Small mammals have been the focus of many studies of insular biology (reviews in: Adler and Levins 1994; Gliwicz 1980; Stamps and Buechner 1985). Not all insular small mammals manifest each component of the island syndrome or the island rule and some populations show mixed patterns. Ebenhard (1990) showed that island populations of the field vole (*Microtus agrestis*) from the Stockholm Archipelago in the Baltic are larger (as expected) but have larger litters and greater reproductive output (contrary to expectations), relative to mainland individuals. Hare (2009) studying mainland and island populations of the bank vole (*Myodes glareoulus*) in the UK, was able to demonstrate population differences in body size (i.e. island populations showing bigger body size), but the author did not find the existence of other classical island syndrome traits: increased densities, more stable densities or a change in the demographic behaviour on islands. Stearns (1976) noted that unexpected patterns in the demographic traits of island rodent populations may be the result of genotype-environment interactions that may change expected island gradients from positive to negative and vice-versa. In addition, some traits like reproductive output and increased densities may vary with time, especially in rodents.

Some of the peculiar demographic characteristics observed on small rodents populations on islands seem to be causally related. In particular, a *higher population density* is likely responsible for the *lower reproductive output* (Adler and Tamarin 1984 for *Peromyscus leucopus*; Drost and Fellers 1991 for *P. maniculatus*), which manifests itself as reduced pregnancy rates, increased aged at sexual maturity, shorter breeding seasons or decreased numbers of reproductive females (Gilbert et al. 1986; Lofgren 1989). However, other demographic characteristics are likely to result from factors that are external to the actual population dynamics. The *increased body* *size* observed in several popoulations of small mammals on islands (Adler and Levins 1994; Gliwicz 1980; Stamps and Buechner 1985) has been explained through a combination of factors, namely competitor release, reduced predator pressure and decreased resource limitations (Lomolino 1985). Larger individuals have greater niche breadths (i.e. can feed on large as well as on small food items) and can therefore exploit resources which elsewhere are used by larger members of that guild; moreover the *competitor release* hypothesis suggests the presence of 'empty' niche space on islands, which will be more easily filled by individuals having a larger size (Lister 1976).

Survival, another demographic characteristic that is different on islands, has been shown to covariate positively with population density, being therefore higher on islands than in mainland populations (Adler and Levins 1994). Higher survival on islands has been attributed to two factors: a more sedentary life style and a lower predation risk. The former has been hypothesized to be the result of the reduced dispersal of individuals from islands and the increased tolerance of conspecifics (by selecting for decreased intra-specific aggressiveness) (Adler and Levins 1994; Crowell 1983; Knell 2009). The reduced predation risk enjoyed by small rodents on islands, besides increasing survival, also leads to less population turnover and hence a smaller variance in the *age structure* of the population which tends therefore to be skewed toward adults compared to mainland populations where turnover is higher (Gliwicz 1980; Salvador and Fernandez 2008).

The demographic characteristic that has received most attention for insular mammals is their tendency to live at *higher densities* relative to their mainland counterparts (Adler 1996; Gliwicz 1980; Salvador and Fernandez 2008; Sullivan 1977). Essentially there are two main hypotheses that attempt to explain this phenomenon:

1. The *Density Compensation Hypothesis* (MacArthur et al. 1972), which explains increased density on islands as a consequence of islands often only having a subset of fauna in comparison to the mainland. It follows that, in the absence of competitors, a single species may have access to additional food and space resources which would otherwise be unavailable in a comparable mainland site (Diamond 1970; Valen 1965; Wilson 1961). Thus, one may expect an increase in the density of this species relative to its mainland sites. The density compensation hypothesis assumes that the abundance and diversity of resources are comparable between mainland and island sites, therefore one would expect that total densities of species within the same competitive guild to be roughly equal between mainland and island sites. However, it is also possible that islands have more resources and hence a higher carrying capacity, in which case one would expect the total densities of species within the same competitive guild on islands to greatly exceed that of a comparable mainland site (termed the *excess density compensation hypothesis*; Case et al. 1979).

2. The *Fence Effect Hypothesis* (Kozakiewicz and Boniecki 1994) which explains that in confined populations, such as those on islands, opportunities for dispersal are likely to be rare. Thus in the absence or reduction of predation pressure, populations of animals may establish very high densities because there is no marginal habitat for them to disperse into (i.e. there is no “dispersal sink”).

The degree of isolation of islands from the mainland is likely to be playing a part in determining the strength of the island syndrome (Adler and Levins 1994), because some of the causes of the demographic differences between islands and mainland depend directly or indirectly on the ability of all species (competitors as well as predators) to disperse to and from islands, which is a function of isolation. Island area is also likely to be important, with larger islands being more mainland-like in terms of habitat and resource availability, as well as the number of competitor, predator and prey species, population densities, etc. Generally the more isolated the population and the smaller the island area, the more pronounced the effects of the island syndrome. Although these tendences have been found in different classes of vertebrates (Goltsman et al. 2005, Novosolov and Meiri 2010; Stamps and Buechner 1985), most data have been obtained for rodents (Adler and Levins 1994 for a review). In this context, it is interesting to test the island syndrome on the populations of the *Apodemus* species on the River Tagliamento, because the degree to which the different insular populations obey the patterns expected from the island syndrome can be taken as an indirect measure of their level of isolation.

This chapter is focused on three of the demographic characteristics that change in insular animals: population density, proportion of adults, and reproductive output. Phenotypical changes in body size of the three species were also investigated. If the island syndrome occurs, the expectation would be for *Apodemus* populations on river islands to exhibit higher densities, larger body size (measured as body weight), a higher proportion of adults and a reduced reproductive output, compared to mainland populations.

4.2 Methods

4.2.1 Study area

For a detailed description of the study area, see chapter 2, section 2.2.

4.2.2 Rodent sampling

Rodent sampling took place over four seasons on 10 islands surrounded by gravel and at three sites of the adjacent mainland. Six large islands (I5, I6, I9, I10, I12 and I18) and four medium islands (I7, I8, I11, I13), varying in size between 0.43ha and 4.17ha were considered for this study. We did not consider small islands in the analysis because in many of them (e.g. I3, I14 and I15 in chapter 2 Figure 2.7) insufficient captures were obtained to investigate if the local populations of the three species were affected by the island syndrome. Sherman traps (Sherman - Tallahassee, FL - USA) were placed in each of the sampled islands and on each of the three sites of the mainland. Traps were set 20m apart and were filled with hay and baited with a mixture of rolled oats and sunflower seeds. On islands, the number of traps was proportional to island size from a minimum of three traps on the smallest island considered to a maximum of 39 traps on the largest island. On the mainland, three areas were investigated and in each area 20 traps were set distributed in two transects of 10 traps each (Figure 2.7 in chapter 2). Further details about the trapping protocol and the pilot data that informed the trapping regime are reported in Chapter 2, section 2.2.

Traps were left in place for three-four days and checked daily in the morning. Captured animals were identified, marked using ear-tags (National Tag & CO - Newport, KY - USA), weighed to the nearest 0.5 g with a Pesola spring balance, sexed, and their breeding condition noted. Females were recorded as imperforate, perforate, lactating, pregnant or having bred. Males were recorded as having abdominal testes or scrotal testes. A sample of the tail was also collected in order to perform genetic analyses on the individuals of *A. sylvaticus* and *A. flavicollis* that had controversial phenotypes and on very young individuals of the two species which had not developed the adult phenotype yet, following the protocol of Michaux et al. (2001) described in detail in Chapter 2, section 2.4.1. Individuals were assigned to two age classes (juveniles and adults) on the basis of weight and reproductive status (Gurnell and Flowerdew 2006).

For each species, the weight of the lightest sexually mature individual captured was taken as a threshold to distinguish between adults and juveniles (all sexually immature). This threshold was set at 15 grams for *A. flavicollis* and *A. sylvaticus* and at 16 grams for *A. agrarius*. Individuals showing weights higher than these thresholds were considered as adults. Other studies used similar thresholds to identify the age classes of these three species (Capizzi and Filippucci 2008; Fasola and Canova 2000; Gliwicz 1988; Montgomery 1980).

Four trapping sessions were carried out, one for each season: May 2010 (spring), September 2010 (summer), November 2010 (autumn) and January 2011 (winter). Further details about the trapping strategy used are reported in Chapter 2, section 2.4.1.

4.2.3 Food resources analysis

In summer 2010, information was collected on the identity and percentage cover of tree and shrub species carrying soft and hard seeds on the mainland, large islands and medium islands. This information provided an estimate of the potential food available for the three species in different habitats. Cover of tree and shrub species carrying seeds was measured according to Braun-Blanquet classes using randomly positioned 10 x 10m quadrats. Proportional to island size, up to 13 quadrats were sampled in each of the studied islands, while on the mainland a total of 19 quadrats were positioned. The tree and shrub species chosen were the dominant ones in the study area: *Acer* sp, *Cornus sanguinea*, *Corlylus avellana*, *Crataegus* sp., *Fraxinus* sp., *Juglans nigra*, *Ligustrum vulgare*, *Prunus* sp., *Rubus* sp., *Quercus* sp. As an index of seed species diversity, the Shannon-Wiener function following Kent and Coker (1992) was calculated for each 10 x 10m quadrat.

4.2.4 Data analysis

As the scope of this chapter is to test the island syndrome, each of the four demographic characteristics that were compared was considered separately on the mainland and on islands (referred to as two different “habitats” in this chapter). All three species were analysed and each species was considered separately. Genetic analyses described in chapter 2 section 2.4.1 were essential for assigning controversial phenotypes to either *A. sylvaticus* or *A. flavicollis* and therefore for the correct attribution of trapped individuals. Statistical analyses were performed using the free Software R (R Development Core Team 2012). Four variables were considered to represent the demographic and phenotypic characteristics of the island syndrome:

(1) Population densities. An index of population density was calculated for each habitat and for each *Apodemus* species. The total number of individuals trapped was normalised by the number of trap nights (TN), as these differed between the two types of habitats.

$$\text{Index of population density} = \frac{total\ number\ of\ individuals\ trapped\ on\ Hi}{total\ number\ of\ TN\ on\ Hi} * 100$$

Where *Hi* is the habitat type, namely mainland or islands.

(2) Proportion of adults (PA). The proportion of adults versus juveniles, with age classes defined by the weight thresholds described above, was calculated for each species and for each habitat.

$$PA = \frac{total\ number\ of\ adults\ captured\ on\ Hi}{total\ number\ of\ TN\ carried\ out\ on\ Hi} \times\ 100$$

Where *Hi* is the habitat type, namely mainland or islands.

(3) Reproductive output (RO). Females were considered breeding if they were pregnant or lactating. Females that had obviously previously produced offspring but were not currently in breeding condition were excluded from this analysis (i.e. those that were not pregnant or lactating but had hairs plucked from around the nipples). Reproductive output was calculated as:

$$RO = \frac{total\ number\ of\ breeding\ females\ captured\ on\ Hi}{total\ number\ of\ TN\ carried\ out\ on\ Hi} * 100$$

Given the low percentage of females in breeding status present in autumn and winter for *A. agrarius*, just data collected in spring and summer were used to evaluate if reproductive output differed between the habitats for this species. For *A. sylvaticus* and *A. flavicollis*, data collected in spring, summer and autumn were used.

(4) Body weight. Individual weights of adult females and males were measured in grams (g).

These four variables were used to explore whether the three mice species under study manifested the island syndrome. Data on population densities, proportion of adults and reproductive output were tested for normality using the Shapiro-Wilk test, checked for homogeneity of variances using Bartlett test and consequently fourth root transformed. Fourth root transformation is the appropriate one when data are positively skewed and when there are a lot of zeros and a few large values (Quinn and Keough 2002, page 65), as in this case.

In order to test the island syndrome, two-way ANOVA was applied on seasonal values of population densities, proportion of adults and reproductive output for each species to understand: (A) whether the factor 'habitat' could explain any of the variations observed (i.e. there was a significant difference in the values of each variable between mainland and islands and if the difference fit the trend predicted by the island syndrome); (B) whether the factor 'season' could explain any of the variations observed; (C) whether there was an interaction between 'season' and 'habitat' in determining these variations. When a significant difference between habitats or among seasons was found for a given variable, Tukey's post-hoc tests were run to carry out pairwise comparisons between its values (i.e. pairwise comparisons between different seasons and/or pairwise comparisons between different habitats).

Unlike the other variables, the variable 'weight' had several values for each site and for each season because it was measured at the individual rather than at the population level, therefore it was decided to analyse it in a different way to avoid losing information by averaging values. For each species, by pooling seasonal and habitat data it was tested whether there were differences in weight between males and females through Mann-Whitney and Wilcoxon tests. The same statistical test was used to check for differences in weight between habitats after the pooling of the seasonal data. Finally, differences in weight between seasons were tested for each species through the Kruskal-Wallis test, after the pooling of the habitat data. When a significant difference between seasons was obtained, Wilcoxon's post-hoc tests were run to check for paiwise comparisons. For the variable 'weight' it was not possible to test whether there was an interaction between seasons and habitats in determining its variations.

In order to evaluate if there was a difference in the value of seed species diversity between the mainland, large islands and medium islands, a Kruskal Wallis Test was applied. Wilcoxon's post-hoc tests were then performed to carry out pairwise comparisons (i.e. pairwise comparisons between different habitats: mainland-large islands, mainland-medium islands, large islands-medium islands).

4.3 Results

4.3.1 Life history variation and island syndrome gradients

In the following sections, results of the ANOVA analyses and of the non parametric tests performed are reported separately for each variable and for each species.

Population densities

For all three species, the two-way ANOVA showed that there was a significant ($p \leq 0.05$) effect of habitat on their population densities (Tables 4.1, 4.2 and 4.3). However, while for *A. flavicollis* and *A. agrarius* this effect consisted of these species having a higher density on the mainland, *A. sylvaticus* showed the opposite trend with higher densities on the islands (Figure 4.1) (Tuckey Post-hoc tests - *A. flavicollis:* mainland densities > island densities: p=0.00; *A. agrarius:* mainland densities > island densities: p=0.02; *A; sylvaticus*: mainland densities < island densities: p=0.00). Therefore while, *A. sylvaticus* showed a trend in population density that followed the predictions of the island syndrome, the other two species went counter to these predictions. Season was also a significant factor in determining the variation in density for these species (Tables 4.1, 4.2 and 4.3), but as there was no interaction between season and habitat (Tables 4.1, 4.2 and 4.3), it means that habitat in itself is an important determinant of densities in these communities. Interestingly, both *A. flavicollis* and *A. agrarius* showed higher densities in spring and summer than in autumn and winter (Tuckey Post-hoc tests: *A. flavicollis* – spring > autumn p=0.04, spring > winter p=0.01, summer > autumn p=0.02, summer > winter p=0.00; *A. agrarius* – summer > winter p=0.04, spring > winter p=0.04) while *A. sylvaticus* differed also in this case with higher densities in spring and winter than in summer (Tuckey Post-hoc tests: spring > summer p=0.05, winter > summer p=0.04).

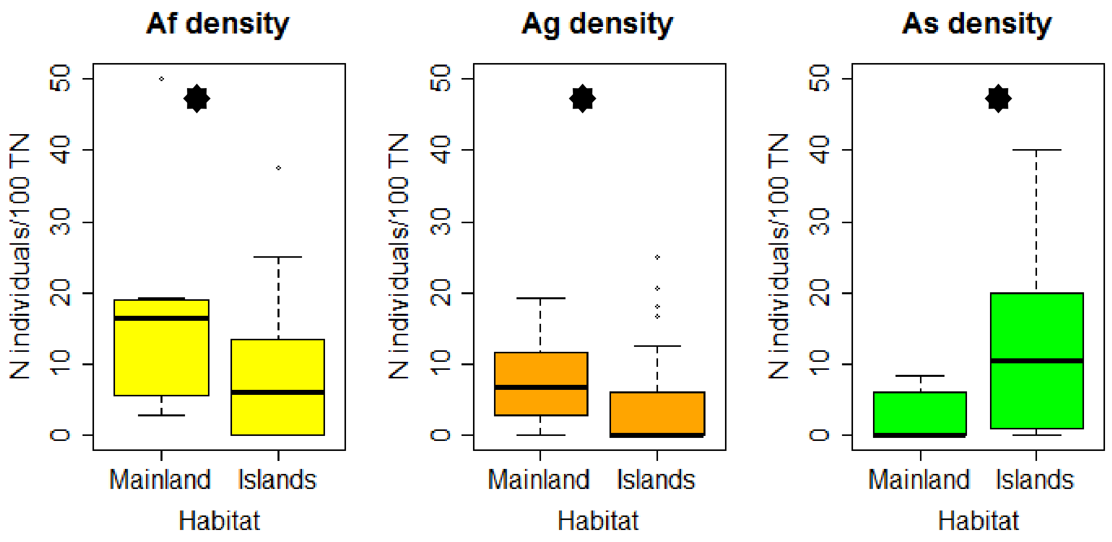


Figure 4.1 Boxplots representing the values of population densities for the three species under study on the mainland and on the islands. Seasonal data were pooled. Af = *A. flavicollis*, Ag = *A. agrarius* and As = *A. sylvaticus*. Black asterisks represent significant differences found between mainland and islands at p≤0.05 level. The median, the first and third quartile and 95% confidence interval of median are represented in each of the boxplots.

Table 4.1 Results of the two-way ANOVA of *A. flavicollis*. MSE stands for the Mean Square Error. Results for the variable weight are reported in the text.

	Habitat (H)			**Season (S)**			**H-S Interaction**		
	F	MSE	p	F	MSE	p	F	MSE	p
Density	$11.10_{(1,44)}$	6.28	0.00	$6.70_{(3,44)}$	3.79	0.00	$1.81_{(3,44)}$	1.02	0.16
Proportion of adults	$13.00_{(1,44)}$	6.40	0.00	$8.46_{(3,44)}$	4.16	0.00	$1.85_{(3,44)}$	0.91	0.15
Reproductive output	$7.39_{(1,33)}$	3.77	0.01	$0.12_{(2,33)}$	0.06	0.88	$3.68_{(2,33)}$	1.88	0.09

Table 4.2 Results of the two-way ANOVA analysis of *A. agrarius*. MSE stands for the Mean Square Error Results for the variable weight are reported in the text.

	Habitat (H)			Season (S)			H-S Interaction		
	F	**MSE**	**p**	**F**	**MSE**	**p**	**F**	**MSE**	**p**
Density	5.73	3.80	0.02	$3.54_{(3,44)}$	2.35	0.02	$0.06_{(3,44)}$	0.04	0.98
Proportion of adults	2.55	1.50	0.18	$6.17_{(3,44)}$	3.63	0.00	$0.09_{(3,44)}$	0.06	0.96
Reproductive output	4.11	0.17	0.05	$0.11_{(1,22)}$	0.02	0.75	$1.02_{(1,22)}$	0.15	0.32

Table 4.3 Results of the two-way ANOVA of *A. sylvaticus*. MSE stands for the Mean Square Error. Results for the variable weight are reported in the text.

	Habitat (H)			Season (S)			H-S Interaction		
	F	**MSE**	**p**	**F**	**MSE**	**p**	**F**	**MSE**	**p**
Density	9.15	6.46	0.00	$3.42_{(3,44)}$	2.42	0.02	$0.91_{(3,44)}$	0.64	0.45
Proportion of adults	4.76	3.67	0.03	$1.88_{(3,44)}$	1.45	0.15	$0.98_{(3,44)}$	0.75	0.41
Reproductive output	1.97	0.17	0.17	$1.32_{(2,33)}$	0.11	0.28	$0.14_{(2,33)}$	0.01	0.86

Proportion of adults

A. flavicollis and *A. sylvaticus* showed a significantly different proportion of adults in the two habitats (Tables 4.1 and 4.3). For *A. flavicollis* the difference was opposite to that predicted by the island syndrome (Tukey'spost-hoc tests: mainland proportion of adults > island proportion of adults, $p<0.01$), while *A. sylvaticus* fitted the gradient of the island syndrome (Tukey's post-hoc test: mainland proportion of adults < island proportion of adults, $p=0.03$)**.** No significant difference was found for *A. agrarius* (Table 4.2). Season was also a factor significantly affecting proportion of adults for *A. flavicollis* and *A. agrarius* (Tables 4.1 and 4.2). For both of these species Tukey's post-hoc tests on seasons indicated that proportion of adults was higher in spring and summer than in autumn and winter (*A. flavicollis:* Tukey's post hoc tests: spring > autumn: $p=0.03$; spring > winter: $p=0.00$; summer > autumn: $p=0.01$; summer > winter: $p=0.00$ – *A. agrarius:* Tukey's's post hoc tests: spring > autumn: $p=0.04$; spring > winter: $p=0.01$; summer > autumn: $p=0.04$; summer > winter: $p=0.00$). No interactions between the factors 'habitat' and 'season' affecting proportion of adults were found for any of the three species.

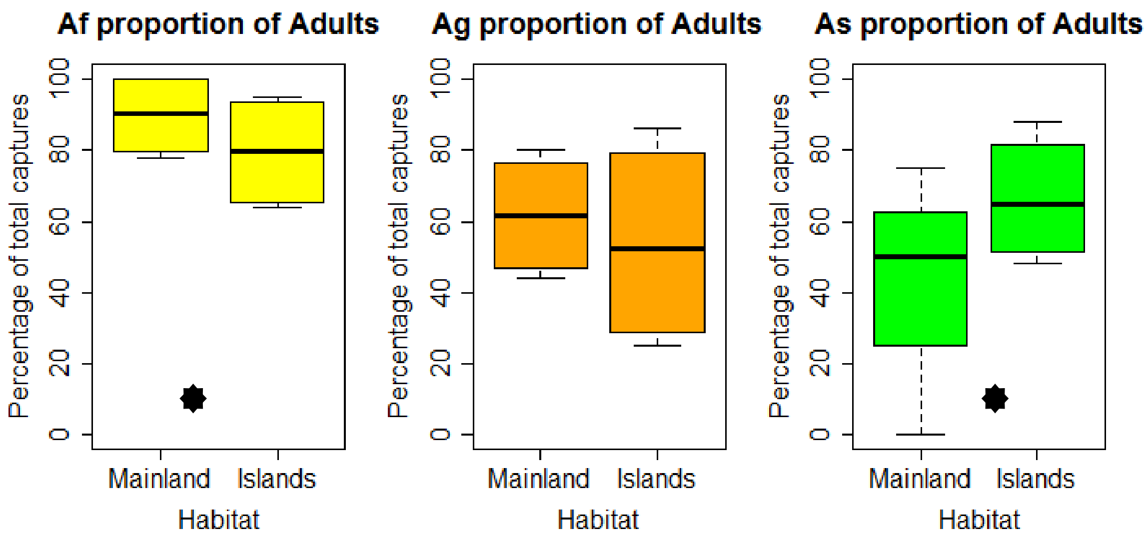


Figure 4.2 Boxplots representing the values of percentages of total adults of the three species under study on the mainland and on the islands. Seasonal data were pooled. Af = *A. flavicollis*, Ag = *A. agrarius* and As = *A. sylvaticus*. Black asterisks represent significant differences found between mainland and island populations. The median, the first and third quartile and 95% confidence interval of median are represented in each of the boxplots.

Reproductive output

The two-way ANOVA revealed that there was a significant difference between the reproductive output of mainland and island populations for *A. flavicollis* and *A. agrarius*, with the gradient fitting the island syndrome predictions (Tables 4.1, 4.2, 4.3 and Figure 4.3) (Tukey's post hoc tests - *A. flavicollis*: number of reproductive females mainland > number of reproductive females islands: p=0.01; *A. agrarius*: number of reproductive females mainland > number reproductive females islands: p=0.05). *A. sylvaticus* demonstrated decreased reproductive output on islands (Figure 4.3), but the two-way ANOVA did not reveal any statistically significant effects of habitat influencing the number of reproductive females present in the two habitats (number of reproductive females mainland > number of reproductive islands: p=0.17). For all three species season was not a factor affecting the reproductive output and no interactions between habitat and season influenced the number of reproductive females captured in the two habitats in different seasons.

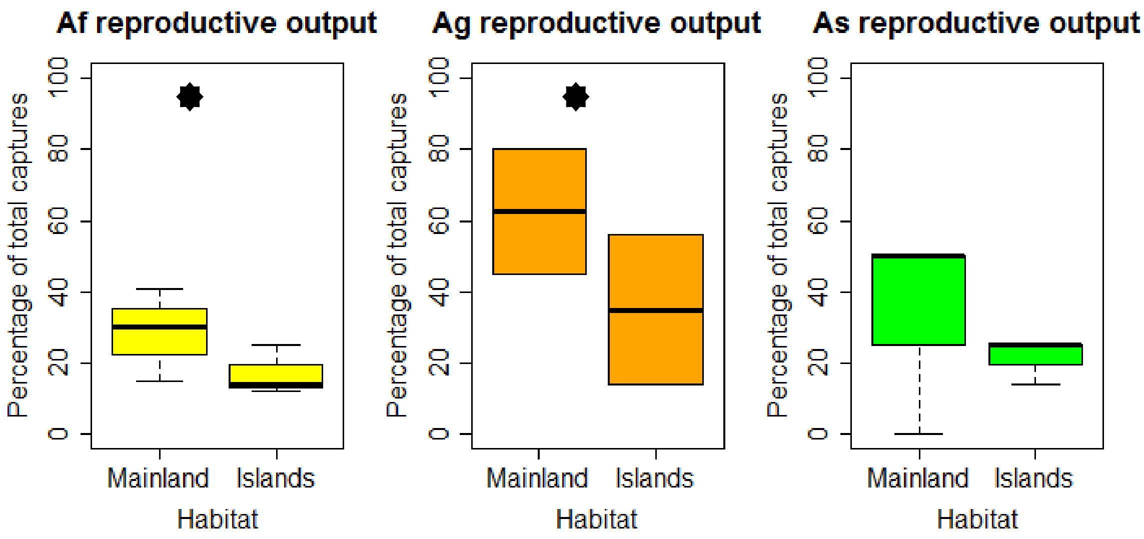


Figure 4.3 Boxplots representing the values of percentages of total breeding females captured for the three species under study on the mainland and on the islands. Seasonal data were pooled. Af = *A. flavicollis*, Ag = *A. agrarius* and As = *A. sylvaticus*. Black asterisks indicate significant differences between mainland and island populations. The median, the first and third quartile and 95% confidence interval of median are represented in each of the boxplots.

Weights

The Mann-Whitney and Wilcoxon tests applied to the pool of seasonal and habitat values of weights did not reveal significant differences between females and males in any of the three species (*A. flavicollis*: W=1624.5, p=1.00; *A. agrarius*: W=444, p=0.38**;** *A. sylvaticus*: W=590.5, p=0.71) (Figure 4.4). None of the three species showed significant differences in weight between mainland and islands, therefore not manifesting evidence for the existence of the island rule in their island population (Mann-Whitney and Wilcoxon test - *A. flavicollis*: W=2305, p=0.13;– *A. agrarius*: W=2305, p=0.13 - *A. sylvaticus*: W=311, p=0.13). Season was a significant factor in determining the variation in weight for *A. flavicollis* (Kruskal-Wallis Chi-Squared=20.91, df=3, p=0.00) and *A. sylvaticus* (Kruskal-Wallis Chi-Squared= 15.44, df=3, p=0.00), but not for *A. agrarius* (Kruskal-Wallis Chi-Squared=5.15, df=3, p=0.16). *A. flavicollis* showed averagely higher weights in summer than spring and winter (Wilcoxon's Post-hoc tests: summer > spring p=0.00; summer > winter p=0.02) For *A. sylvaticus* summer weights were significantly higher than autumn and winter weights (Wilcoxon's Post-hoc tests: summer > autumn p=0.00, summer > winter p=0.00).

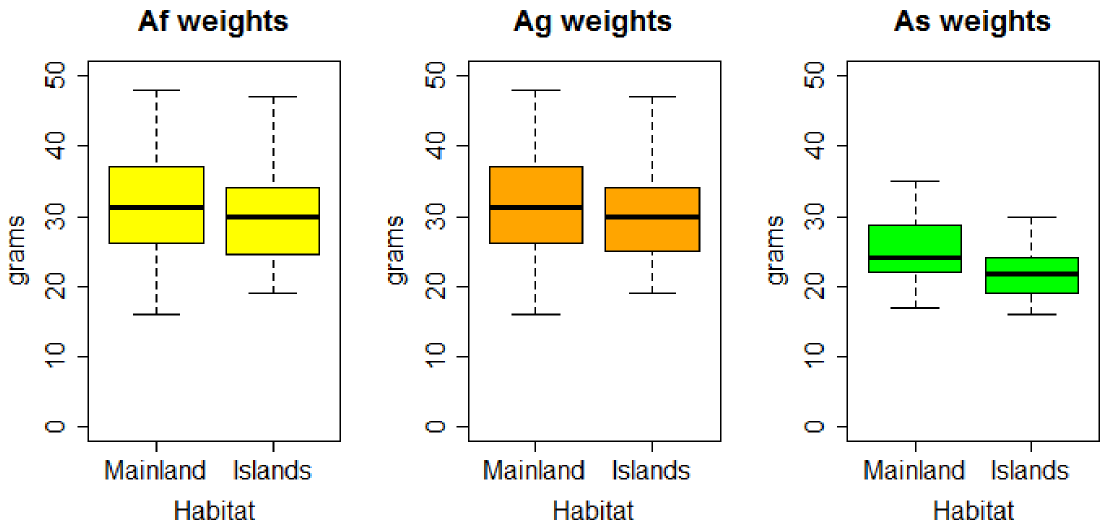


Figure 4.4 Boxplots representing the values of weights for the three species under study on the mainland and on the islands. Seasonal data were pooled. Af = *A. flavicollis*, Ag = *A. agrarius* and As = *A. sylvaticus*. The median, the first and third quartile and 95% confidence interval of median are represented in each of the boxplots.

In summary, the species that most consistently followed the predictions of the island syndrome for the variables analysed was *A. sylvaticus*, which demonstrated increased densities and an increased proportion of adults on islands compared to the mainland (Figure 4.5). *A. flavicollis* and *A. agrarius* showed patterns that were opposite to the predictions of the island syndrome, apart from reproductive output, with a higher output on the mainland than on islands (Figure 4.5). None of the three species showed a difference in weight between mainland and islands, therefore not reflecting the trends for gigantism observed in other small mammal species living on islands.

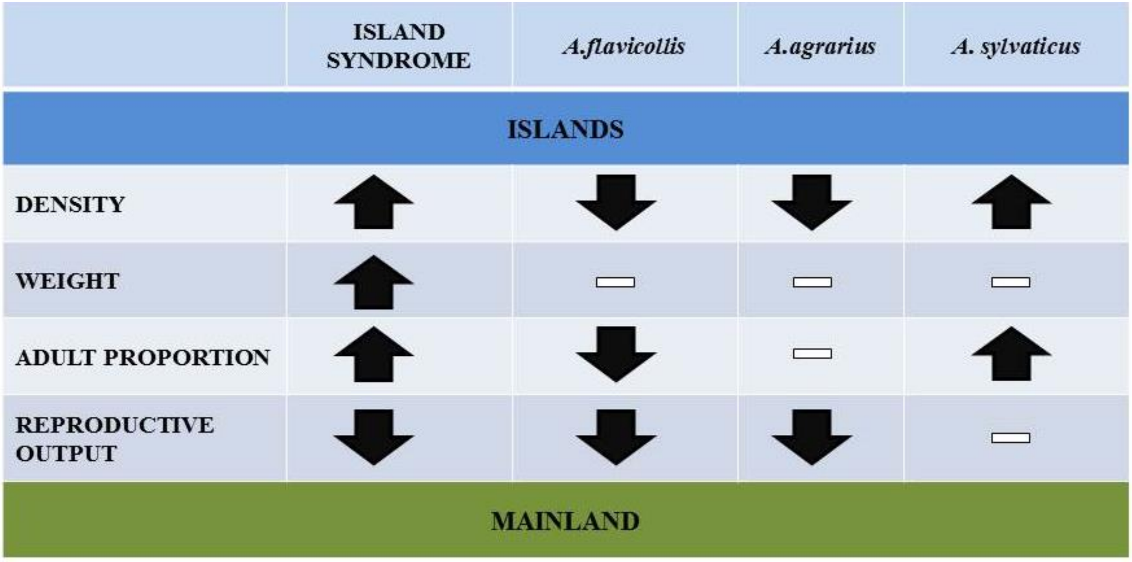


Figure 4.5 Variables used to understand whether the three *Apodemus* species manifested the island syndrome. Differences in the mean annual values of the four variables among mainland and islands (area>0.1 ha) were investigated through ANOVA (N=44). Black arrows of the *ISLAND SYDNROME* column describe patterns typical of island populations manifesting the syndrome (e.g. an arrow pointing up for the variable density means that on islands rodent densities are usually higher than on mainland). In the columns *A. flavicollis, A. agrarius* and *A. sylvaticus*: black arrows indicate significant differences found in the investigated variables between mainland and islands. White rectangles indicate no significant differences.

4.3.2 Food resources analysis

Seed species diversity differed significantly among mainland, large islands and medium islands (Kruskal-Wallis Chi-squared=21.92, df=2, $p<0.01$). By running the Wilcoxon's tests for pairwise comparisons between habitats, the differences were found to be significant between all habitats (mainland-large islands $p=0.00$, large islands-medium islands $p=0.04$, mainland-medium islands $p<0.00$), with the mainland having the highest diversity, followed by large and medium-sized islands respectively (Figure 4.6).

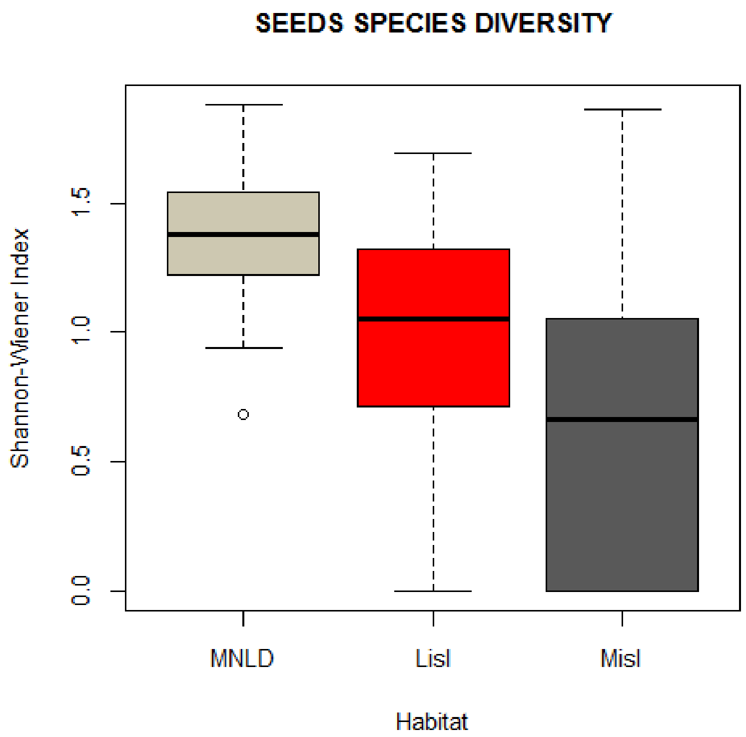


Figure 4.6 Boxplots with the values of Seed species diversity (Shannon-Wiener function) obtained for the mainland, large islands and medium islands. The black line of each boxplot represents the value of the median. MNLD=mainland, Lisl= large islands, Misl=medium islands. The median, the first and third quartile and 95% confidence interval of median are represented in each of the boxplots.

4.4 Discussion

4.4.1 Density compensation in the Apodemus community of Tagliamento river islands

This study found evidence to support the hypothesis that river island populations of *A. sylvaticus* on the Tagliamento floodplain manifested some of the traits typical of the island syndrome, while populations of *A. flavicollis* and *A. agrarius* did not. *A. sylvaticus* is arguably the most insular species of all the three in the study area. Indeed, if we take the percentage of total captures as a measure of how much each species is present on the mainland and on islands, *A. sylvaticus* was captured in 75% of all capture events on islands, compared to 57% for *A. flavicollis* and 42% for *A. agrarius*. On the mainland, *A. sylvaticus* was captured in 42% of all capture events, while for *A. flavicollis* this was 100% and for *A. agrarius* 83%.

Islands represent a perennial habitat for *A. sylvaticus*, and this species is present on islands throughout the year, while the other two species tend to be present only in certain seasons (Appendix 4.1). On islands, *A. flavicollis* was captured more often in spring and summer than autumn and winter and a similar result was obtained also for *A. agrarius*, suggesting that islands act as a temporary dispersal habitat, more than as a source habitat for these two species. This hypothesis finds confirmation in the trends of adult versus juvenile proportions found in this study for the three species, on islands compared to the mainland. Juveniles usually form the dispersing portion of a population. *A. sylvaticus* showed a higher population density and a higher proportion of adults versus juveniles on islands. On the contrary, the other two species, besides showing decreased density on islands, also manifested a lower proportion of adults versus juveniles on islands. Besides the natality and mortality of individuals, the possibility for juveniles to disperse between habitat patches might constitute one of the ways of controlling numbers in patch populations (Kozakiewicz 1993). Kozakiewicz and Szacki (1987) observed that in some local populations of small mammals, emigration rates can greatly exceed immigration rates, and in consequence, cause a reduction in their densities. Moreover, habitat persistence is an important determinant of the rate of dispersal. Dispersal is indeed expected to be favoured in temporal and ephemeral habitats, as species need to be able to track intermittent resources which encourage movements of organisms (Travis and Dytham 1999).

The island syndrome traits found for *A. sylvaticus* on the Tagliamento floodplain might be explained mainly through a mechanism of *density compensation.* *A. sylvaticus* is a habitat generalist and opportunist and is found in all types of forest habitats and seral stages throughout its range, while *A. flavicollis* is a habitat specialist and seems to prefer mature and closed forests (Gurnell 1985; Montgomery 1985). *A. agrarius* has a diet quite similar to *A. flavicollis* and in conditions of low densities, the species is common in riparian forests, while at high densities, the species also colonizes agricultural fields, woodlands and meadows (Zeida 1967). There may be competition for resources (i.e. food and space) among the three species, which would result in changes in their numbers and distribution and in habitat segregation. For example, Hoffmeyer and Hansson (1974) showed that *A. flavicollis* suppressed the number and hence influenced the density and distribution of *A. sylvaticus* in forest and abandoned field habitats in southern Sweden. Hansson (1971) also found that *A. flavicollis* ate food very similar to that of *A. sylvaticus*, and, being the dominant species (Montgomery 1978), might lower the amount of food available to the smaller *A. sylvaticus*.

Inverse relationships in numbers between *Apodemus spp.* were also found in other studies in Europe: Holisova and Orbtel (1979) found that numbers of *A. sylvaticus* in a spruce forest in Czechoslovakia were highest when numbers of *A. flavicollis* were lowest. It is therefore arguable that on the mainland, where the diversity and abundance of soft and hard bearing seed species is higher in respect to the islands (Figure 4.6) and where *A. flavicollis* meets all its habitat requirements, this species dominates; on islands, *A. flavicollis* has a lower density, a lower reproductive output and a lower adult proportion and this would let *A. sylvaticus* reach higher densities. The flexibility in the diet of *A. sylvaticus* and the reduced competition with *A. flavicollis* presumably promote its higher densities on the Tagliamento river islands, despite their suboptimal condition in terms of food availability.

As for *A. agrarius*, it is a species subordinate to the other two, whose population dynamics are strongly affected by the other *Apodemus* species present in the community (Gliwicz 1984). According to Gurnell (1985), *A. sylvaticus* and *A. agrarius* are quite similar in many respects and especially in their being subordinate to *A. flavicollis*. In habitats where *A. agrarius* co-occurs with *A. flavicollis*, it shows higher mortality and emigration and lower survival of offspring (Gliwicz 1981). It is likely than on islands, where food resources are less available in respect to the mainland, this species suffers more the competition with the other two: indeed, among the three *Apodemus* species present in the study area, *A. agrarius* was the one showing the lowest values of density on islands (Figure 4.1). Nonetheless it is also likely that the lack of significant differences between the measured demographic characteristics of *A. agrarius* was due to the general low densities obtained for the species, especially on islands.

Despite the density compensation of *A. sylvaticus,* river islands seem to be a sub-optimal habitat for the all *Apodemus* species under investigation; indeed, even if not significantly, all the three species showed a trend for a decreased weight and a decreased reproductive output on islands. These trends are likely due to the fact that on islands diversity and availability of food resources is lower than on the mainland (Figure 4.6), therefore excluding the excess density compensation as a mechanism explaining the island syndrome traits found for *A. sylvaticus*.

The *fence effect*, by which dispersal is hampered by island isolation, has also been suggested as a possible process promoting island syndrome (Adler and Levins 1994). However, results obtained from this thesis (chapters 3 and 5) suggest that the fence effect could not often occur on the Tagliamento islands. Radio-tracking on *A. agrarius* carried out in summer 2010 (results in chapter 5, Figures 5.3 and 5.4) revealed that males of this species are able to cross the islands edges and travel through the gravel matrix in their day-time and night time movements. Data from seasonal trapping suggests that inter-island movements also happen for the other two species in spring and early summer: a total of 18 individuals (N=12 *A. sylvaticus*, N=6 *A. flavicollis*) which were the first time captured on a given islands, in the following trapping days or trapping season were re-captured on a different island (average length of inter-island movement=270m±99, range: 70-425m, N=14 individuals moving in spring N=4 in early summer). The reason for relatively high movement rates between islands is that water is often absent between these two habitats, making the matrix relatively permeable to dispersal. Water is particularly scarce in the matrix in late spring and summer, when a relatively high proportion of dispersing individuals probably occurs and inter-islands movements are fairly easy. Potentially the fence effect could occur for short periods in conditions of very high flow, when islands are completely surrounded by deep and fast flowing water (like some of the investigated islands during mid-autumn or early winter floods, Figure 2.3 in chapter 2) and therefore crossing the matrix is not possible. It can be therefore concluded that *density compensation* is the most plausible mechanism able to substantially explain the island syndrome patterns found for *A. sylvaticus*.

4.4.2 Quantification of the timespan to develop island syndrome traits

Much of the literature investigating the manifestation of the island syndrome in small mammals has focused on islands which formed thousands of years ago during the last glacial period or even before (e.g. Adler 1996; Hare 2009; Libois et al. 1993; , Russel et al. 2011). Given that island populations analysed here are presumably very recent, this study can be considered as a first step towards the quantification of the minimum time needed to develop some aspects of the island syndrome in small mammals. The Tagliamento islands under study were 40 years old at most (chapter 2, section 2.1.1), and results presented here show that already after 40 years we can observe some aspects of the island syndrome in *A. sylvaticus.* No other study to our knowledge has investigated the island syndrome in animals living in temporal and ephemeral habitats like river islands. In this study, it was shown that there is a completely different relative composition in the *Apodemus* community living the mainland (more stable habitat) and the islands (more ephemeral habitat) of the Tagliamento floodplain, due to a difference in the relative population density of the three *Apodemus* species. On the mainland the species which dominates and is present with the highest densities is *A. flavicollis*, followed by *A. agrarius* and *A. sylvaticus*. On the islands it is *A. sylvaticus* which predominates followed by *A. flavicollis* and *A. agrarius* (Figure 4.1). This indicates that for some rodent species like *A. sylvaticus* the ecological processes described by MacArthur and Wilson (1967) affecting densities traits of island communities, could occur also in this kind of environment and could develop over a relatively short time frame. Another study carried out by Aponte et al. (2003), revealed that densities of Amazonian tortoises (*Geochelone carbonaria*) on an artificial lake island of Lago Guri in Venezuela, were higher on the island than on the mainland just 16 years after the island was created as a consequence of hydroelectric impoundment, further suggesting that rapid adjustments in population are possible in insular fauna.

While population density and age structure seem to respond to the conditions found on islands relatively quickly, no evidence was found for an effect on body weight in this study. The reason of this difference may be in the time needed for these different parameters to change. Schmidt and Jensen (2005) report changes in body size of Danish mammals and birds in response to landscape fragmentation in Denmark within relatively short periods of time (e.g. 175 years). Adler and Levins (1994), in describing the mechanisms driving the island syndrome in rodent populations, argue that long-term changes in body weight may represent many generations of directional selection following colonization or isolation. Under such conditions, long-term directional selection may produce locally adapted island populations that phenotypically differ from mainland populations (Lomolino 2005). Changes that occur within the lifetime of a single individual occurring within an island population following initial colonization, may only be initial micro-evolutionary responses to the novel selection pressures (Kozakiewcz et al. 2009). However, if these initial micro-evolutionary responses are periodically disturbed by stochastic events like floods, new traits are periodically re-set and the time span for them to be reflected in visible changes in the phenotype is obviously longer. Moreover, islands considered in this study are quite close to each other and to the mainland, increasing the chance of inter-island and mainland-island movements by small mammals and therefore the possibility for continuous re-colonization events of sites where the local small populations went stochastically extinct, and also of inter-mixing of different populations.

Wijnhoven et al. (2005), studying the impact of flooding on a small mammal population inhabiting the floodplain of a regulated enbanked river in the Netherlands, found that recolonization after a flood can be a very slow process which depends on the mobility of the species, on the number of colonization sources and the number of survivors from which a population must recover. The Tagliamento floodplain still conserves geomorphological features and flow conditions at a near-pristine level. The natural variation in elevations in pristine rivers, like in the Tagliamento, normally creates a whole range of flooded and non-flooded biotopes. Water levels rise more gradually and have lower peaks, compared to embanked floodplains, leaving fauna more opportunities to escape and survive during a flood (Andersen et al. 2000). The periodical possibility of immigration from the mainland and of emigration of local populations to non-flooded areas could also somehow slow down the development of micro-evolutionary changes which could lead to proper changes in body size.

4.4.3 Conclusions

The most important finding of this study is that some traits of the island syndrome in rodents, like an increased density and an increased adult proportion can be manifested in ephemeral islands, even after very short time since their isolation, but just in those species which have perennial populations on islands, like *A. sylvaticus* on the river islands of the Tagliamento. *A. sylvaticus* has a variable life history that can adapt to such spatially and temporally heterogeneous environment and that facilitates rapid exploitation of such heterogeneity. Given that the other two species constituting the *Apodemus* community in the study area do not thrive in these habitats or are strongly affected in their population dynamics by the other members of the community, river islands would act as “refugia” for *A. sylvaticus.* Moreover, this study highlights how island populations which are not permanently isolated from the mainland and whose dynamics are often disturbed by stochastic events, do not show island syndrome traits like a modified body size: such modification of the phenotype would probably require more time or conditions where island isolation is permanent and time since isolation is longer.

4.5 References

Adler, G.H., 1996. The island syndrome in isolated population of a tropical forest rodent. Oecologia 108, 694-700.

Adler, G.H. and Levins, R., 1994. The island syndrome in rodent populations. Quarterly Review of Biology 69, 473-490.

Adler, G.H. and Tamarin, R.H., 1984. Demography and reproduction in island and mainland white-footed mice (Peromyscus leucopus) in souther-eastern Massachusetts. Canadian Journal of Zoology 62, 58-64.

Aponte, C., Barreto, G.R., Terborgh, J., 2003. Consequences of habitat fragmentation on age structure and life history in a tortoise population. Biotropica 35, 550-555.

Angerbjörn, A., 1986. The Evolution of Body Size in Mammals on Islands: Some Comments. American Naturalist 125, 304-309.

Capizzi, D. Filippucci, M.G., 2008. Apodemus agrarius, In Fauna d'Italia: Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia. eds G. Amori, L. Contoli, A. Nappi. Edizioni Calderini, Milano.

Case, T. J., Gilpin, M. E., and Diamond, J. M., 1979. Overexploitation, Interference Competition, and Excess Density Compensation in Insular Faunas. The American Naturalist 113, 843-854.

Crowell, K.L., 1983. Islands - Insight or Artifact?: Population Dynamics and Habitat Utilization in Insular Rodents. Oikos 41, 442-454.

Diamond, J.M., 1970. Ecological consequences of island colonization by Southwest Pacific Birds, I. type of niche swifts. Proceedings of the National Academy of Sciences USA 2, 529-536.

Drost, C.A. and Fellers, G.M., 1991. Density cycles in an island population of deer mice, Peromyscus maniculatus. Oikos 50, 347-352.

Ebenhard 1990. A colonization strategy in field voles (*Microtus agrestis*): reproductive traits and body size. Ecology 71, 1833-1848.

Fasola, M. and Canova, L., 2000. Aymmetrical competition between the bank vole and the wood mouse, a removal experiment. Acta Theriologica 45, 353-365.

Foster, B.L., 1964. Evolution of mammals on islands. Nature 202, 234-235.

Gilbert, B.S., Krebs, C.J., Talarico, D., Cichowski, D.B., 1986. Do *Clethryonomys rutilus* females suppress maturation of juvenile females. Journal of Animal Ecology 55, 543-552.

Gliwicz, J., 1980. Island populations of rodents - their organization and functioning. Biological Reviews of the Cambridge Philosophical Society 55, 109-138.

Gliwicz, J., 1981. Competitive interactions within a forest rodent community in central Poland. Oikos 37, 353-362.

Gliwicz, J., 1984. Competition among forest rodents: effects of Apodemus flavicollis and Clethrionomys glareolus on A. agrarius. Acta Zoologica Fennica 172, 57-60.

Gliwicz, J., 1988. Seasonal dispersal in non-cyclic populations of Clethrionomys glareolus and Apodemus flavicollis. Acta Theriologica 33, 263-272.

Gurnell, J., 1985. Woodland rodent communities. Symposia of the Zoological Society of London 55, 377-411.

Gurnell, J. and Flowerdew, J. R., 2006. Live Trapping Small Mammals 4th edition. The Mammal Society London UK.

Hansson, L., 1971. Small rodent food, feeding and population dynamics. A comparison between granivorous and herbivorous species in Scandinavia. Oikos 22, 183-198.

Hare, E., 2009. In School of Biological Sciences. Queen Mary University London, Island syndrome in rodents : a comparative study on island forms of the bank vole, Myodes glareolus –

Heaney, L.R., 1978. Island area and body size of insular mammals: evidence from the tri-colored squirrel (Callio-sciurus prevosti) of Southwest Africa. Evolution 32, 29-44.

Hoffmeyer, I. and Hansson, L., 1974. Variability un number and distribution of Apodemus flavicollis and A. sylvaticus in S. Sweden. Z. Saugetierk 39, 15-23.

Holisova, V. and Obrtel, R., 1979. The food eaten by Clethrionomys glareolus in a spruce monoculture. Folia Zoologica 28, 219-230.

Knell, R.J., 2009. Population density and the evolution of male aggression. Journal of Zoology 278, 83-90.

Kozakiewicz 1993. Habitat isolation and ecological barriers. The effect on small mammal populations and communities. Acta Theriologica 38, 1-30.

Kozakiewicz, M. and Szacky, J., 1987. Small mammals in isolated habitats - islands on the mainland or island populations only? Wiad. Ekol. 33, 31-45 (In Polish with English summary).

Kozakiewicz, M., Gortat, T., Panagiotopoulou, H., Gryczynska-Siemeakowska, A., Rutkokwsi, R. Kozakiewicz, A., Abramovicz, K., 2009. The spatial genetic structure of the bank vole (myodes glareolus) and yellow necked mouse (Apodemus flavicollis) populations: The effect of distance and habitat barriers. Animal Biology 59, 169-187.

Libois, R., Fons, R. and Bordenave, D., 1993. Mediterranean small mammals and insular syndrome: Biometrical study of the long-tailed field mouse (Apodemus sylvaticus) (Rodentia-Muridae) of Corsica. Bonn Zoological. Bullettin. 44, 147-163.

Lister, B.C., 1976. The Nature of Niche Expansion in West Indian Anolis Lizards II: Evolutionary Components. Evolution 30, 677-692.

Lofgren, O., 1989. Do intrinsic or extrinsic factors limit reproduction in cyclic populations of *Chethrionomys glareoulus* and *C. rufocanus*? Holoarctic Ecology 12, 54-59.

Lomolino, M., 1985. Body size of mammals on islands: The island rule reexamined. The American Naturalist 125, 310-316.

Lomolino, M.V., 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32, 1683-1699.

MacArthur, R.H. and Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press.

MacArthur, R.H., Diamond, J.M., Karr, J.R., 1972. Density compensation in island faunas. Ecology 53, 330-342.

Michaux, J.R., Kinet, S., Filippucci, M.G., Libois, R., Besnard, A., Catzeflis, F., 2001. Molecular identification of three sympatric species of wood mice (Apodemus sylvaticus, A. flavicollis, A. alpicola) in western Europe (Muridae: Rodentia). Molecular Ecology Notes 1, 260-263.

Michaux, J.R., De Bellocq, J.G., Sarà, M., Morand, S., 2002. Body size increase in insular rodent populations: A role for predators? Global Ecology and Biogeography, 11, 427-436.

Goltsman, M., Kruchenkova, E. P., Sergeev, S., Volodin I., Macdonald, D.W., 2005. 'Island syndrome' in a population of Arctic foxes (*Alopex lagopus*) from Mednyi Island**.** Journal of Zoology (*Lond.)* 267, 405-418.

Montgomery, W.I., 1978. Intra- and interspecific interactions of Apodemus sylvaticus (L.) and A. flavicollis (Melchoir) under laboratory conditions. Animal Behaviour 26, Part 4, 1247-1254.

Montgomery, W.I., 1980. Population structure and dynamics of sympatric Apodemus species (Rodentia: Muridae). Journal of Zoology 192, 351-377.

Montgomery, W.I., 1985. Interspecific competition and the comparative ecology of two congeneric species of mice, In Case Studies in Population Biology. ed. L.M. Cook, pp. 126-187. Manchester University Press, Manchester.

Novosolov, M. and Meiri S., 2010. The effect of island type on lizard reproductive traits. Journal of Biogeography 40, 2385-2395.

Quinn, G.P. and Keough, M.J., 2009, 8th ed. Experimental Design and Data for Biologists. Cambridge University Press, Cambridge, UK, 537pp.

Reyment, R.A., 1983. Palaeontological Aspects of Island Biogeography: Colonization and Evolution of Mammals on Mediterranean Islands. Oikos 41, 299-306.

Russell, J.C., Ringler, D., Trombini, A., Le Corre, M., 2011. The island syndrome and population dynamics of introduced rats. Oecologia 167, 667-676.

Salvador, C.H., Fernandez, F.A.S., 2008. Population dynamics and conservation status of the insular cavia intermedia (Rodentia:Cavidae). Journal of Mammalogy 89, 721-729.
Schmidt, N.M., Jensen, P.M., 2005. Concomitant patterns in avian and mammalian body length changes in Denmark. Ecology and Society 10, 5, 8 p.

Shanker, K. and Sukumar, R., 1998. Community structure and demography of small-mammal populations in insular montane forests in southern India. Oecologia 116, 243-251.

Stamps, J.A. and Buechner, M., 1985. The territorial defense hypothesis and the ecology of insular vertebrates The Quartely Review of Biology 60, 155-181.

Sullivan, T.P., 1977. Demography and dispersal in island and mainland populations of the deer mouse, Peromyscus maniculatus. Ecology 58, 964-978.

Travis, J.M. and Dytham, 1999. Habitat persistence, habitat availability and the evolution of dispersal. Proc. R. Soc. Lond. 266, 723-728.

Valen, L.V., 1965. Morphological Variation and Width of Ecological Niche. The American Naturalist 99, 377-390.

Van Valen, L., 1973. Pattern and the balance of nature. Evolutional Theory 1, 31-49.

Wilson, E.O., 1961. The Nature of the Taxon Cycle in the Melanesian Ant Fauna. The American Naturalist 95, 169-193.

Appendix 4.1

Values of population density (Individuals captured7100 Trap Nights) obtained in each season in each site of the study area for the three *Apodemus* species object of this study. HAB= Habitat (MNLD=mainland, L=large islands in red, M=medium islands in black, S=small islands in blue); Patch=Patch ID; SPR=spring, SUM=summer, AUT=autumn, WINT=winter, NA= no data available because the site was not trapped. Only mainland, large island and medium island values of density were analysed in this chapter.

		A. flavicollis				***A. agrarius***				***A. sylvaticus***			
HAB	**Patch**	**SPR**	**SUM**	**AUT**	**WINT**	**SPR**	**SUM**	**AUT**	**WINT**	**SPR**	**SUM**	**AUT**	**WINT**
MNLD	M1	17.86	19.35	18.60	2.78	14.29	19.35	13.95	2.78	7.14	6.45	0.00	0.00
MNLD	M2	50.00	18.75	50.00	8.11	2.78	6.25	0.00	0.00	0.00	0.00	0.00	2.70
MNLD	M3	15.12	3.13	11.11	2.78	7.50	9.38	8.33	2.78	0.00	0.00	5.56	8.33
M	I1	0.00	14.28	0.00	NA	0.00	28.57	20.00	NA	16.67	0.00	20.00	NA
S	I2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	50.00	50.00	50.00
S	I3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100.00	50.00	0.00	0.00
S	I4	100.00	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	33.33	0.00
L	I5	16.67	18.75	0.00	0.00	5.56	0.00	0.00	0.00	16.67	6.25	12.50	11.76
L	I6	14.08	17.24	10.87	8.06	8.45	20.69	1.09	3.23	14.08	0.00	2.17	12.90
M	I7	0.00	0.00	9.09	0.00	0.00	25.00	0.00	0.00	40.00	0.00	9.09	40.00
M	I8	10.00	20.00	0.00	0.00	0.00	0.00	0.00	0.00	40.00	0.00	33.33	40.00
L	I9	4.55	10.53	6.67	25.00	18.18	10.53	6.67	10.00	9.09	0.00	6.67	15.00
L	I10	16.67	12.50	0.00	0.00	16.67	0.00	0.00	0.00	16.67	0.00	0.00	20.00
M	I11	0.00	25.00	0.00	0.00	0.00	0.00	0.00	0.00	20.00	25.00	33.33	0.00
L	I12	13.04	12.00	0.00	4.17	0.00	4.00	0.00	0.00	4.35	4.00	20.00	8.33
M	I13	37.50	25.00	0.00	0.00	25.00	12.50	0.00	0.00	0.00	0.00	20.00	36.36
S	I14	0.00	0.00	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
S	I15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M	I16	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M	I17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	33.33	11.11
L	I18	12.50	5.56	0.00	0.00	5.56	5.56	5.56	0.00	8.50	5.56	16.67	0.00
M	I19	0.00	0.00	0.00	NA	0.00	0.00	0.00	NA	40.00	40.00	0.00	NA

Chapter 5 - Home ranges of male *Apodemus agrarius* in a riparian landscape: consequences of resource availability and edge effects

Abstract

Resources and competitors are known to strongly affect the size and shape of individual home ranges in mammals, but the presence of habitat edges within home rages can also be a determinant factor. From the standpoint of acquiring food resources to maximize energy efficiency, an individual should occupy the smallest home range possible. In areas where resources are distributed homogeneously home ranges can be relatively small, but where resources are patchy an individual must increase home range size to incorporate sufficient high quality patches to provide the necessary resources.

In this chapter, the size of home ranges and core areas of male individuals of the striped field mouse, *Apodemus agrarius*, inhabiting continuous riparian forest were studied using radio-tracking methods and compared to those of individuals inhabiting nearby islands on the River Tagliamento in Italy, considered to represent patchy habitats. Only males were the object of this study because, in *Apodemus* species, these have been observed to travel more than females, especially in the breeding season when females are territorial, and therefore their spatial behaviour should be particularly sensitive to the structure and spatial patterning of a particular habitat.

Edge habitats, availability of resources, and densities of *A. agrarius*, alongside its conspecifics *A. flavicollis* and *A. sylvaticus*, were investigated as potential factors determining the size of home ranges and size and number of core areas.

Results indicate that, on average, the home ranges and core areas of island individuals were, respectively, four and five times larger than those living on the mainland. The number of core areas was not different between the mainland and the islands, but the distances between core areas were longer on the islands. Linear models indicate that distance of the centre of the home range from edge habitat and resource availability are the two most important factors in explaining the variation in home range size of the radio-tracked individuals.

Studies of other vertebrates in mainland-island systems found that home ranges tend to be larger on the mainland than on islands, which is the opposite to that found in this study. The trends observed in this study are therefore discussed in the context of the peculiar ecological and structural habitat conditions found on the Tagliamento mainland-island system.

5.1 Introduction

Home ranges are the areas in which animals acquire necessary resources and carry out biological requirements for life (Burt 1943). Within these areas some parts will be used more intensively, others less so. These intensively used parts within the home range of an individual are called core areas (Hodder et al. 1998). The size of home range in mammals has been shown to depend on a variety of factors such as the amount and distribution of food (Arthur et al. 1996; Bowers et al. 1990; Senft et al. 1987; Stradiotto et al. 2009), competition (Bond and Wolff 1999), predation risk (Morris et al. 2011), cover (Tufto et al. 1996), density and individual differences such as age, sex and breeding condition (Mares and Lacher 1987). With respect to food, animals tend to range over larger areas when food is patchily distributed (O'Neill et al. 1988; Relyea et al. 2000; Tufto et al. 1996). Furthermore, some evidence suggests also that the presence of habitat edges within home ranges affects their size at patch and landscape scale. In some birds, for example, larger home ranges are often found at the edges of isolated habitat patches, while home ranges are smaller in patch interiors (Krebs 1971).

In this chapter, male individuals of the striped field mouse, *Apodemus agrarius*, were studied by means of radio-tracking to explore whether there were differences in the spatial behaviour between mice inhabiting the riparian forest (hereafter called *mainland*) and those inhabiting the islands and to identify the factors that might determine such differences. It was decided to concentrate the study on males only as these usually travel more than females, especially in the breeding season when females are territorial (Wolff 1993), and therefore they should be particularly sensitive to the structure and spatial patterning of a particular habitat.

The home range characteristics of individuals living on the mainland and individuals living on islands were compared and three factors in particular were taken into account to attempt to explain differences: the density of competitors, the abundance of resources, and the presence of habitat edges within home ranges.

The *population density* of conspecifics and of species that occupy a similar niche are known to affect the characteristics of the home range in mammals (Barreto et al. 2000; Salek et al. 2015; Yunger 2004). No radio-tracking study has ever been carried out on *A. agrarius,* but a study investigating its spatial behaviour through capture–mark–recapture techniques, revealed that its spatial behaviour can be strongly affected by the density of competitors such as the yellow necked mouse, *Apodemus flavicollis* (Vukicevic-Radic et al. 2006). These authors observed that in a habitat where *A. agrarius* coexisted with *A. flavicollis* an increase in the size of the home range of *A. agrarius* was concurrent to a reduction of the density of the two species. In general, such a negative relationship may be attributed to food availability (Mares et al. 1982), or to interactions among individuals restricting each other's movement at higher densities, although in most studies it has been difficult to separate these effects (Boutin 1990). When *A. agrarius* and *A. flavicollis* coexist in the same area, it has been shown that density of *A. agrarius* decreases and emigration rates of sexually mature individuals increase (Gliwicz 1981; Ylonen et al. 1991). According to Mayeikyte (2002), *A. flavicollis* is dominant over *A. agrarius* and they likely compete by interference and aggression.

Radio-tracking studies on *A. sylvaticus* and *A. flavicollis* have shown that home range size varied in relations to factors such as resource abundance (Rosalino et al. 2011b; Stradiotto et al. 2009) and population density (Wilson et al. 1993). Stradiotto et al. (2009) reported a negative relationship between population density and home range size in male *A. flavicollis* and other studies on similar species in the USA reported similar trends (Falls et al. 2007; Merritt et al. 2001).

The *abundance of resources* is another factor that is known to affect home range characteristics (Tucker et al. 2014). Where resources are more abundant per unit area, home range has been shown to be smaller. Among rodents for example, Corriale et al. (2013) in Argentina, observed a significant negative linear correlation between home range size and estimators of food availability (i.e. percentage cover of grasses, graminoids and green plant material) in capybaras (*Hydrochoerus hydrochaeris*). A similar result was obtained by Stradiotto et al. (2009) for *A. flavicollis* in a beech woodland in Central Italy. Home range size changed seasonally and home ranges were larger in periods of lower beech seed abundance. Moreover, resource distribution as well as abundance could have an effect on the characteristics of home ranges. In patchy habitats, species may increase home range size and use multinuclear core areas to incorporate sufficient high quality patches in a home range that also includes large amounts of matrix or less preferred habitat (Constible et al. 2006; Selonen et al. 2001 Siffczyk et al. 2003; Sunde and Redpath 2006).

Finally, the presence of *habitat edges* within their home range may have an effect on the characteristics of home ranges in mammals (Harrington et al. 2001). The term *"edge"* identifies the border between two habitat types (Collinge 2009, page 94). *Edge effect* (in relation to organism dynamics) describes the extent to which the boundary between the two habitats influences movement of individuals within and between-patches (Forman and Godron 1981). A study on small mammals in fragmented experimental landscapes revealed that individuals living close to habitat edges have larger home ranges than individuals living in patch interiors (Bowers et al. 1996). Explanations for this edge effect were related to mechanisms of home range defence and changes in density: lower defence costs due to fewer neighbours and thus larger home ranges were found near habitat edges than in more crowded habitat interiors (Stamps et al. 1987). Preferential foraging at edges has been observed in root-voles (*Microtus oeconomous*) inhabiting small woodland fragments when home range of single individuals encompassed edge areas (Hovland et al. 1999). In large continuous areas, where no preference for edge foraging was found, more habitat area was available so that fewer home ranges included edges.

In accordance with these observations, it was expected that home range size of *A. agrarius* would increase in size for those animals that live in areas where the density of conspecifics and competitors is lower, where food resources are scarcer and which live close to habitat edges rather than for those animals living in habitat interiors. It has been shown in chapter 4 that the population density of *Apodemus* spp. was greater on the mainland and that food resources were more abundant on the mainland than on the islands; it was therefore expected that both home ranges and core areas of male *A. agrarius* would be larger on the islands. Moreover, given the expected increased size of home ranges on islands, it was expected that the number of core areas of animals living on islands would be higher than those living on the mainland because island animals had to find several places for shelter during their daily and nightly movements in order to decrease the predation risk. It was also expected that home ranges on islands incorporated more habitat edges, as habitat is more fragmented on islands, therefore predicting that home ranges should be even larger on islands due to this effect.

5.2 Methods

5.2.1 Study site

This study was conducted in the near-natural dynamic floodplain of the River Tagliamento, in the eastern Alps in Italy. The main study area was the active tract of an island-braided floodplain complex and the nearby mainland that fringed the active tract (Figure 5.1). For a detailed description of the study area, of the vegetation community and of the mechanism of island formation, see chapter 2, section 2.2 and Figure 2.7.

Three sites on the mainland and three on the islands of the braided tract were selected for this study. The three sites of the mainland were coded as M1, M2 and M3 and they were more than 500m distant from each other (Figure 5.1). The three sites on the islands were located on large island I6 (two sites I1 and I2) and on large island I9 (site I3). These island sites were >350m distant from each other and ≤200m from the mainland (Figure 5.1). Island sites were selected taking into consideration the maximum size and width of the islands (i.e. they had to be enough wide to host 7x7 trapping grids. with 10m between trap points, which was placed to estimate the density of the three *Apodemus* species, see below). Individuals were radio tracked at all six sites and the population density of *Apodemus* spp. and the abundance of food resources were measured at all sites.

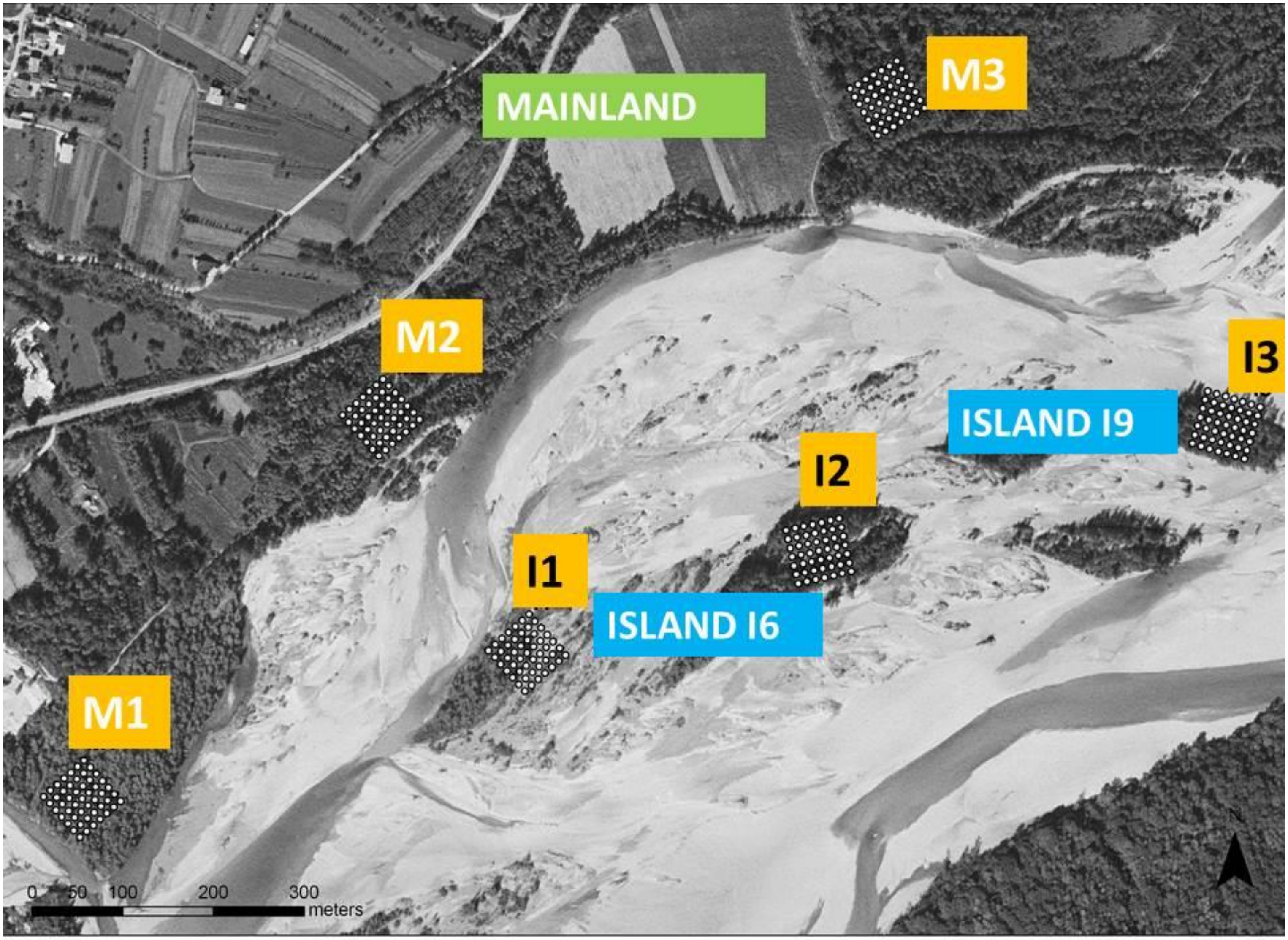


Figure 5.1 Study area and location of the trapping sites in the mainland (M1, M2 M3) and on the islands (I1, I2, and I3).

5.2.2 Radio tracking

Sherman Traps (Sherman Tallahassee - FL, USA) baited with sunflower seeds and rolled oats were used to capture small mammals. Animals trapped were individually marked using ear-tags (National Tag & CO – Newport, KY - USA), weighed, sexed and aged following the protocol of Gurnell and Flowerdew (2006). Some of the animals trapped were subsequently radio-tracked in three consecutive sessions from June to September 2010. In each session, one single site on the mainland and one site on the islands were investigated. Sampling lengths for each session were the same: four trapping days followed by ten tracking nights.

After each four-days trapping session, non-transient animals weighing at least 28 grams were fitted with a radio-transmitter (BD-2C; Holohil Systems Ltd. Carp, Ontario, Canada) mounted on a nylon cable-tie collar. To minimize the inclusion of transient mice in the data-set, individuals were radio-collared only if they were trapped a minimum of three times per trapping session (Raska-Jurgiel 2001). The weight of the complete transmitter package was <2g which was less than 5% of the adult body mass as recommended by Wolton and Trowbridge (1985). All collared animals were released at the point of capture. A total of 22 males of *A. agrarius* were fitted with a radio-collar.

Circadian activity of *A. agrarius* changes during the course of the year, being mainly nocturnal in the summer, diurnal and nocturnal in autumn and mainly diurnal in winter (Kryštufek 1991). Mice have been shown to have a unimodal activity through the night at 20˚C with a broad peak covering all the night hours from 6pm to 6am; at 5˚C mice showed a bimodal activity, after the first peak of activity during the first hours of darkness (6pm-10pm), there is a second distinct peak during the hours before dawn

(2am 6 am) (Tertil 1972). After each trapping session, the radio-collared animals were tracked during ten nights, five evening-shifts (16:00 h - 00:00 h) and five night-shifts (20:00 h - 04:00 h). These shifts were chosen on the basis of the described peaks found in the literature (see above), “corrected” on the basis of a five day pilot study on two animals conducted in May 2010. These pilot data revealed that the first peak of activity could start as early as 16:00 while the second peak rarely finished later than 04:30 in the morning.

Radio-collared animals were located using Sika Biotrack receivers (Biotrack Ltd., UK), together with three element flexible Yagi antennas (Biotrack Ltd, UK). Animals were located through triangulation by two or three operators working simultaneously in different positions estimated with GPS. The time interval between two triangulations on the same animal was 45 minutes; this time interval was sufficiently short to locate each mouse and long enough to avoid autocorrelation of the data (Otis and White 1999; Rooney et al. 1998). When possible, successive fixes on the same animal were taken from the same positions (landmarks): in this way the GPS coordinates of the tracker were taken several times over the same night (or over successive nights); the average values of the GPS coordinates were then calculated to achieve a more accurate measure of the locations of the trackers, reducing the error associated with the GPS.

Home ranges were analysed only for those animals that showed an asymptotic curve in a plot of the cumulative number of fixes taken each day versus home range size (Harris et al. 1990). This was the case for eight animals on the mainland and nine animals on the islands. Five radio-collared individuals disappeared from the study populations (they were presumably killed), before a sufficient number of fixes was collected.

5.2.3 Home range estimation

To compare the characteristics of home ranges of males between the two habitats, home range size and core area size were estimated and the number of core areas counted. Home range size was determined using the 95% fixed kernel method with a least-square cross validation to select the smoothing parameter (Kernohan et al. 2001). To calculate core area size, the kernel function at a 50% level was applied (Harris et al. 1991). Kernel probability distributions and their relative 95% and 50% probability surfaces were calculated using Arcview 3.2 (ESRI 1992).

5.2.4 Factors affecting home range characteristics

Three factors affecting the home ranges of male *A. agrarius* were considered: the population density of all *Apodemus* spp. (*A. agrarius, A. flavicollis, A. sylvaticus*), an index of food availability based on percentage tree cover, total number of shrubs with a dbh>10cm, total number of shrubs carrying seeds with a dbh>10cm, and habitat edge effects.

Apodemus spp. population densities

The trapping sessions used to select individuals for radio-tracking were used also to estimate the densities of the *Apodemus* spp. populations in the area. In order to estimate animal densities, a 7x7 trapping grid was set with 10m between trap points (total grid area=0.36 ha, Figure 5.1) at each of the six sites. Traps were active for four days and checked every early morning. The Minimum Number of Animals known to be alive

(MNA) (Krebs 1999) during each trapping session, was used as an estimate of the density of *A. agrarius*, *A. flavicollis* and *A. sylvaticus*. A value of *overall population density* was also obtained for each the three sites of the mainland and of the islands, by summing up the values of MNA obtained for the three species at each site. Previous studies on a wide range of small mammal populations have shown that these estimates are consistently close to true small mammals densities (Boutin et al. 2006; Wauters et al. 2004).

Estimation of resource availability

The sampling of the vegetation was carried out concurrently to the trapping of the animals. A total of 16 2x2m quadrats were sampled within each trapping site for an overall of 48 quadrats sampled on the mainland and 48 on the islands. Each quadrat was centred on every third trap point. For each of the quadrats, three habitat variables were recorded and considered as surrogates for estimating availability of plant food (i.e. seeds and plant material) for the three *Apodemus* species.

(1)*Percentage of tree cover* was measured on each 2x2m quadrat. Tree cover was defined as the cover of vegetation >8 m.

(2)*Total number of all shrubs with a diameter at breast height (dbh)>10cm* were counted in each 2x2m quadrat (hereafter called *number of all shrubs*). Shrubs were higher than >2m and lower than trees.

(3)*Total number of shrubs bearing hard and soft seeds with a dbh>10cm* were counted in each 2x2m quadrat (hereafter called *number of shrubs with seeds*). The species selected for the calculation of the value of this variable were: *Cornus sanguinea*, *Corlylus avellana*, *Crataegus* sp., *Fraxinus* sp., *Juglans nigra*, *Ligustrum vulgare*, *Prunus* sp., *Rubus* sp., *Quercus* sp., *Tilia sp*., *Robinia pseudoacacia* since they are known to occur in the diet of *A. agrarius* (Holisova 1967).

Edge effects

In the Tagliamento floodplain, animals should be more influenced by the presence of edge habitat on the islands than on the mainland, given that islands are completely surrounded by open gravels or by water channels. In order to evaluate whether the spatial behaviour of animals was affected by edge effects, the *minimum distance of the centre of the home range (kernel 95% estimator) from the closest habitat edge* was measured, both on the mainland and on the islands. Arcview 3.2 (ESRI 1992) Geographical Information System tools were used to measure this distance on aerial images of the study area in winter 2009.

5.2.5 Statistical analyses

Assumptions of normality and of homogeneity of variances in the sampled data of home range and core area size, distance between core areas, as well as in the data describing resource availability and edge effects were investigated respectively with Shapiro-Wilk tests and Bartlett's tests. Values of home range and core area size in each of the two habitats were not normally distributed. Therefore, in order to test whether home range and core area sizes were larger on islands than on the mainland a non-parametric Mann-Whitney and Wilcoxon test was applied (N=8 animals on the mainland and N=9 in the islands). The difference in the size of home ranges and core areas within each of the three sites at the two habitats, mainland and islands, was also tested using the non-parametric Kruskal-Wallis test (N=3 sites in each habitat). Given the low sample size and the fact the data were not normally distributed, the difference in the number of core areas for individuals living on the mainland and those living on islands was tested through the Mann-Whitney and Wilcoxon test. The values of *distances between core areas* within each individual's home range in each habitat showed a normal distribution, but the variances of the two samples were not homogeneous. Therefore a parametric test, namely the Welch Two Samples t-test, was applied to check for differences in the values of distance in-between core areas between the two habitats (N=7 values of distance on the mainland and N=11 values of distance on the islands).

Values of overall population density at the two habitats were visually analysed and compared to the mainland/islands patterns in density found in chapter 4. The values of the variables describing resource availability in the mainland and on the islands (i.e. *percentage of tree cover*, *number of all shrubs*, and *number of shrubs with seeds*) were not normally distributed. Consequently, to compare the values of these variables in the two habitats, the non-parametric test of Mann-Whitney and Wilcoxon test was applied (N=48 quadrats on the mainland and N=48 on the islands). The values of the variable *distance of the centre of the home range from the closest habitat edge* showed a normal distribution, but the variance of the mainland sample was not equal to the variance of the island sample. Therefore the values of this variable were compared between the two habitats through a Welch Two Samples t-test (N=8 animals on the mainland and N=9 in the islands).

To investigate factors that could explain home range and core area size, home range size and total core area size for each individual (N=17) were regressed against the three independent variables of *overall population density*, *number of shrubs with seeds*, and *distance of the centre of the home range from the closest habitat edge* (i.e. full models). For this analysis, only the *number of shrubs with seeds* has been presented from amongst the resource availability variables as this is the one that is likely to be the most representative of food availability for *A. agrarius*. Measures of *overall population density* and of *number of shrubs with seeds* were taken from the closest trapping sites in respect to the home range and core area size of the radio-tracked animal. When one home range covered more than one sampling site for trapping and vegetation quadrats, the values of each of these two variables were averaged between the different sites. In order to meet the assumptions of the multiple regression (i.e. normal distribution of residuals and linear relations between continuous variables), a logarithmic transformation of the dependent variable was used.

The predictors which resulted to be not significant were then removed and the regressions were then re-run to identify the most parsimonious models explaining variations of home range size and core area size. Values of adjusted R^2 were calculated for all the models. Normality of residuals was tested through the Shapiro-Wilk test. All the statistical analyses were performed using R version 2.14.2 (R Development Core Team 2012).

5.3 Results

5.3.1 Home range characteristics in the two habitats

A total of 63 individuals of *A. agrarius* were trapped and of those 22 were fitted with radio collars, 11 on the mainland and 11 on islands (Table 5.1). The mean number of fixes per animal was the same for the mainland (38±6 fixes, N=8 individuals) and islands (38±9 fixes, N=9 individuals). It took on average 7.7±1.2 days (N=17 individuals) for the home range of individuals to reach an asymptote in its size (Figure 5.2), which was within the ten days of radio tracking that were carried out for each individual.

Although sample sizes are small, home range and core area sizes did not differ significantly among the three sites of the mainland or among the three sites of the islands (Table 5.2). The values for home range size and core area size obtained for each tracked individual are reported in Appendix 5.1. There was a significant difference between home range size and core area size between mainland and islands (Table 5.2; Figures 5.3, 5.4, Figure 5.5). On average, home ranges of island animals were four times larger than those of mainland animals, while core areas of animals living on islands were five times bigger than those living on the mainland (Table 5.2). On the mainland out of the eight tracked individuals, four had one core area, two had two core areas and two had three core areas. On the islands, out of the nine radio-tracked individuals, four had one core area, two had two core areas and three had three core areas. The number of core areas did not differ between mainland and islands (Table 5.2, Appendix 5.1).

Table 5.1 Variables measured in the three trapping sites of the mainland (M1 to M3) and of the islands (I1 to I3). *Population density variables*: Minimum Number of Animals captured alive (MNA) of *A. agrarius* (Ag), of *A. flavicollis* (Af) and *A. sylvaticus* (As) and *overall population density*. *Resource availability variables*: Tree cover = Mean Percentage of tree cover (±SD), N shrubs 10cm dbh=*mean number of all shrubs* (±SD) counted in the grid; N shrubs bearing seeds>10cm dbh=mean *number of shrub with seeds* (±SD) counted in each grid. Number of animals monitored via radio-tracking is indicated in the last column; number of radio-collared individuals used to estimate home range size is given in parentheses.

	POPULATION DENSITY				*RESOURCE AVAILABILITY*			
	MNA Ag	***MNA Af***	***MNA As***	***Combined population density***	***Tree cover***	***N shrubs > 10 cm dbh***	***N shrubs bearing seeds > 10 cm dbh***	***Radiotracked individuals (home range estimation)***
M1	22	7	3	32	88 ± 25	3.6 ± 1.7	1.8 ± 1.4	3 (3)
M2	33	21	2	56	76 ± 32	3.3 ± 1.7	1.9 ± 1.5	4 (2)
M3	12	8	0	20	36 ± 38	5.3 ± 2.4	2.6 ± 1.6	4 (3)
I1	11	7	1	19	21 ± 29	3.3 ± 2.9	0.3 ± 0.6	4 (4)
I2	12	8	6	26	57 ± 39	3.3 ± 2.3	0.5 ± 0.9	3 (1)
I3	11	12	0	33	47 ± 42	3.2 ± 1.5	0.9 ± 1.4	4 (4)

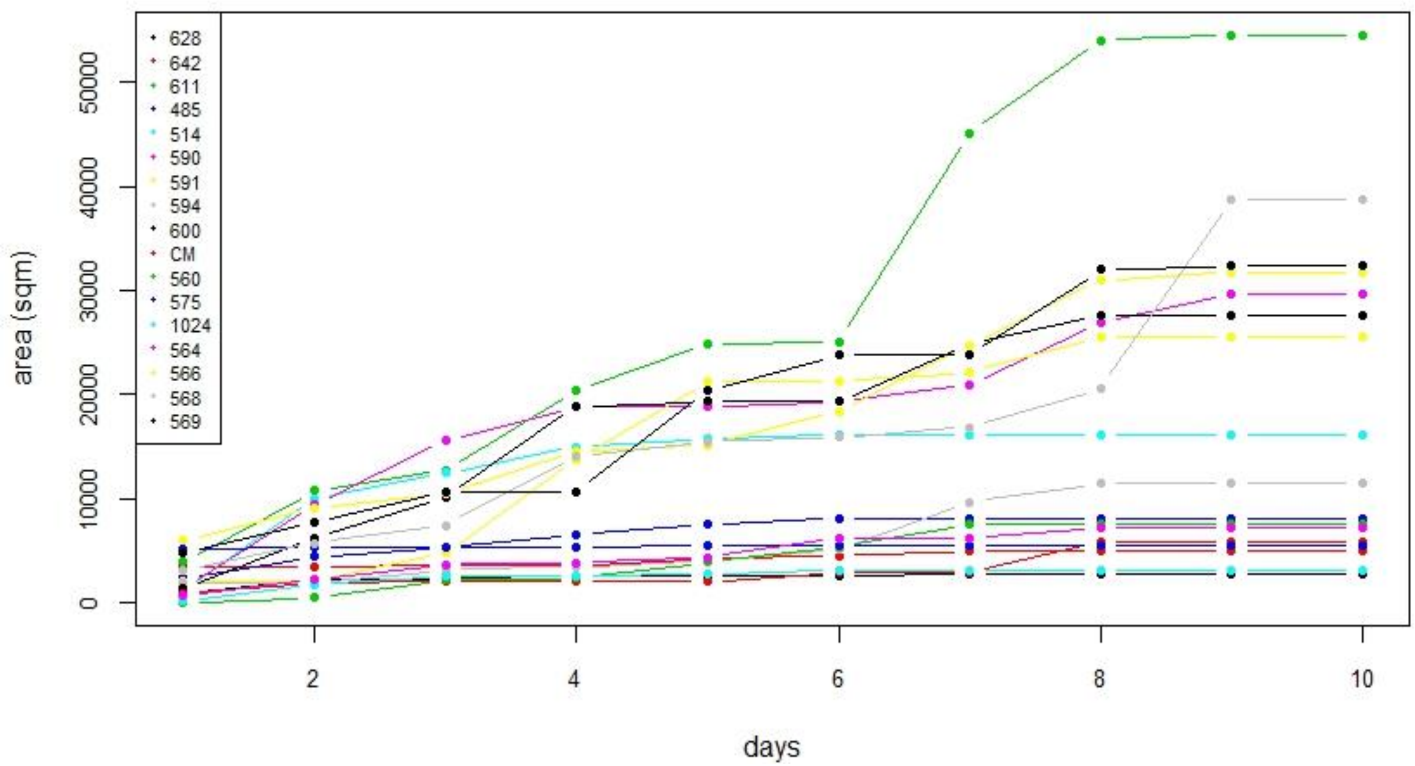


Figure 5.2 Asymptotic curves of the number of days individuals of *A. agrarius* were radio-tracked versus home range size. In the legend the ID identifying each individual is reported (see Appendix 5.1 for information regarding where each animal was trapped and radio-tracked). Number of animals whose home ranges were analysed was eight on the mainland and nine on the islands.

Table 5.2 Summary statistics for home range area (95%) and total core area (50%) and number of core areas for each site and habitat. Test statistic - the Kruskall Wallis test was used to compare sites within islands or mainland; the Mann-Whitney-Wilcoxon test was used to compare all sites in mainland with all sites in island habitats. P = p-value.

Range area	Habitat	Site	Mean	Stdev	Median	IQR	N	Test Statistic	P
95	Island	I1	2.3	0.86	2.7	1.50	4	3.5	0.18
	Island	I2	5.4		5.4		1		
	Island	I3	2.7	1.38	3.2	2.33	4		
	Mainland	M1	1.0	0.53	0.8	1.00	3	4.6	0.11
	Mainland	M2	0.4	0.14	0.4		2		
	Mainland	M3	0.5	0.20	0.5	0.40	3		
95	Island	All	2.9	1.4	3.0	1.70	9	4.0	0.00
	Mainland	All	0.7	0.4	0.6	0.43	8		
50	Island	I1	0.3	0.12	0.3	0.23	4	2.7	0.26
	Island	I2	0.8		0.8		1		
	Island	I3	0.5	0.30	0.5	0.58	4		
	Mainland	M1	0.1	0.11	0.1	0.20	3	0.6	0.76
	Mainland	M2	0.1	0.06	0.1		2		
	Mainland	M3	0.1	0.04	0.1	0.08	3		
50	Island	All	0.4	0.26	0.4	0.50	9	7.0	0.00
	Mainland	All	0.1	0.07	0.1	0.08	8		
No. core areas	Island	All	1.9	0.93	2.0	2.0	9	33.0	0.80
	Mainland	All	1.7	0.89	1.5	1.8	8		

Figure 5.3 Home ranges and core areas (dashed areas) of individuals of *A. agrarius* tracked on the mainland sites M1 and M2 and on the islands sites I1 and I2. In the legend, numbers identify the ID of each radio-tracked animal.

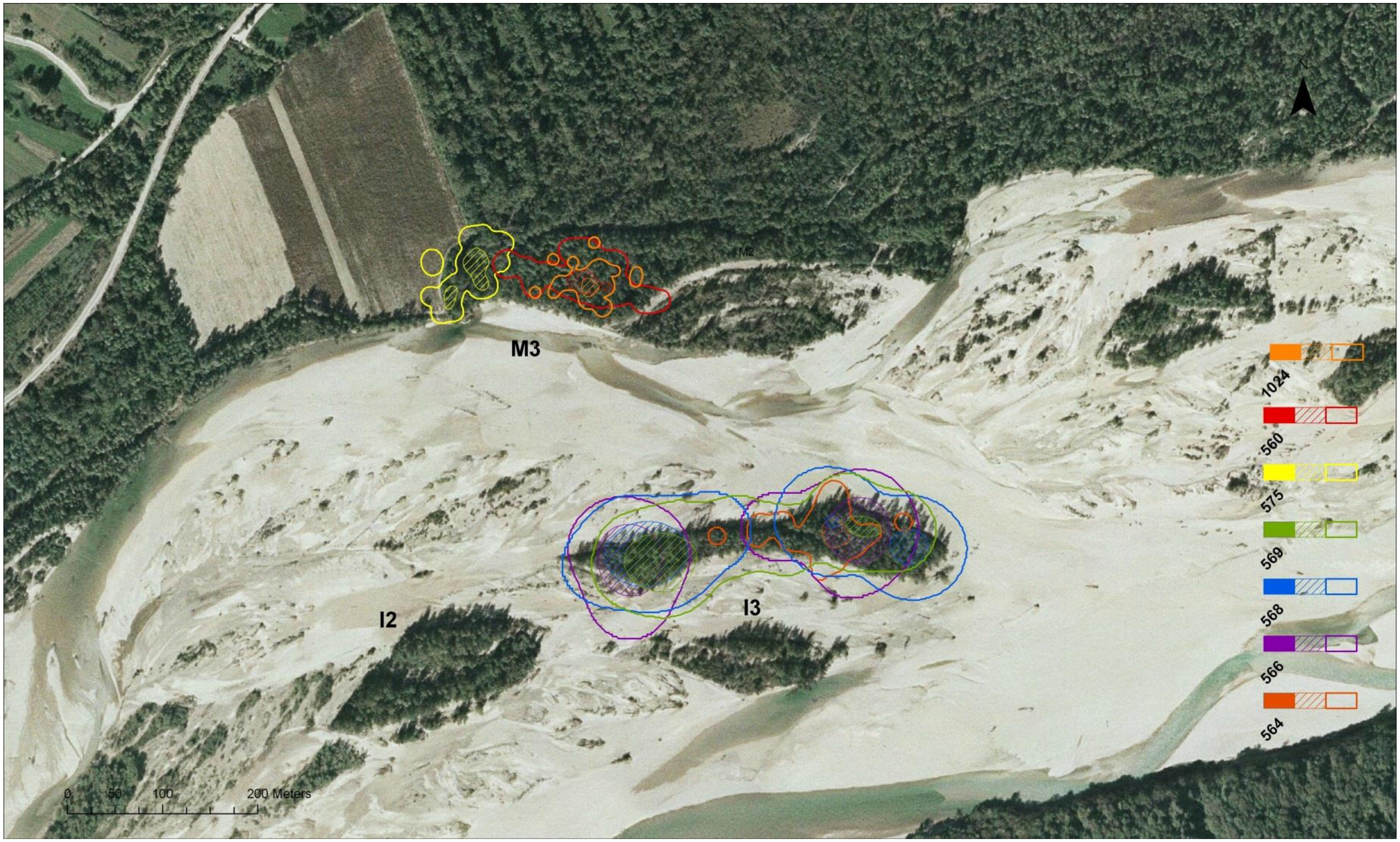


Figure 5.4 Home ranges and core areas (dashed areas) of individuals of *A. agrarius* tracked on the mainland site M3 and on the island site I3. In the legend, numbers identify the ID of each radio-tracked animal.

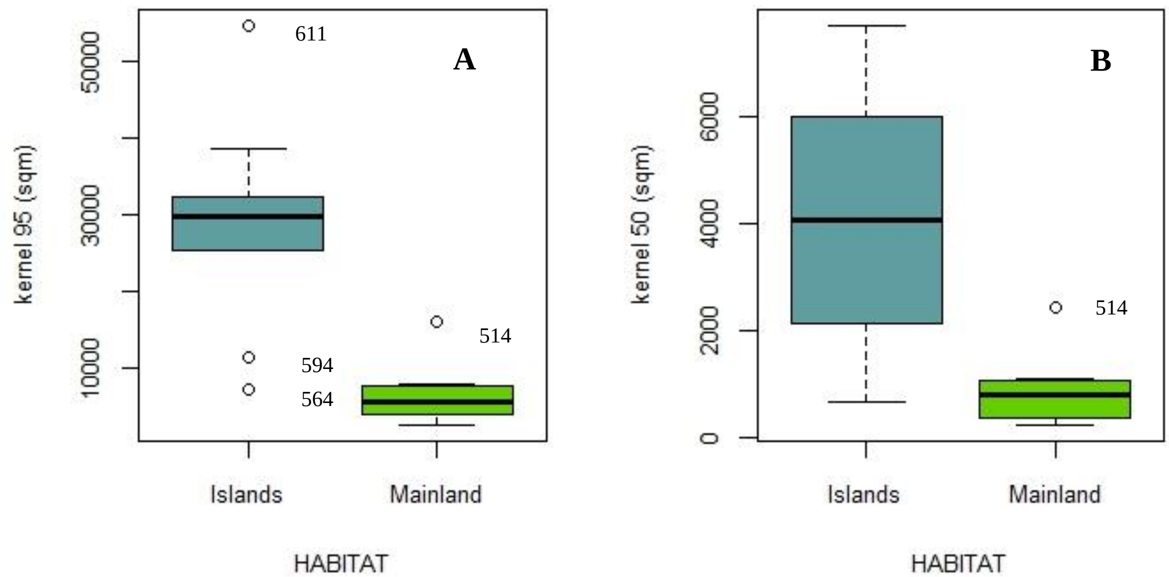


Figura 5.5 Box plots representing the distribution of values obtained for (A) home range size (kernel 95) and (B) core area size (kernel 50) on the mainland and on the islands. Bold lines in the boxplots represent the median. Circles represent the outliers numbered according to the ID of the each individual (see Appendix 5.1).

The average distance between core areas of the same individual was 65m±24 on the mainland and 160m±68 on islands, the difference being significant (Welch Two Sample t-test; t=-3.56, df=14.46, $p<0.01$, N=7 values of distance on the mainland and N=11 values of distance on the islands).

5.3.2 Population densities of *Apodemus* spp. in the two habitats

Confirming the results of the trapping transects in chapter 4, the values of densities of *A. agrarius* obtained with the trapping grids showed a decreasing trend moving from the mainland to the islands. For *A. flavicollis* this trend was not completely confirmed, as there was a site on the mainland (i.e. M1) which showed comparable values of density with those obtained on the islands (Tables 5.1 and 5.3 - Average values - *A. agrarius*: Mainland=22.3±10.5, *Islands*=11.3±0.6, *A. flavicollis*: Mainland=12.0±9.0, Islands=7.8±2.7, N=3 grids on the mainland and N=3 grids on the islands). As for *A* *sylvaticus*, very few individuals were trapped within the grids (Table 5.1) both on the mainland and on the islands therefore it was not possible to compare densities obtained with the grid with those obtained with transects. When considering the *overall population density* from all three species combined, there was a lower density on the islands and less variation (Figure 5.6).

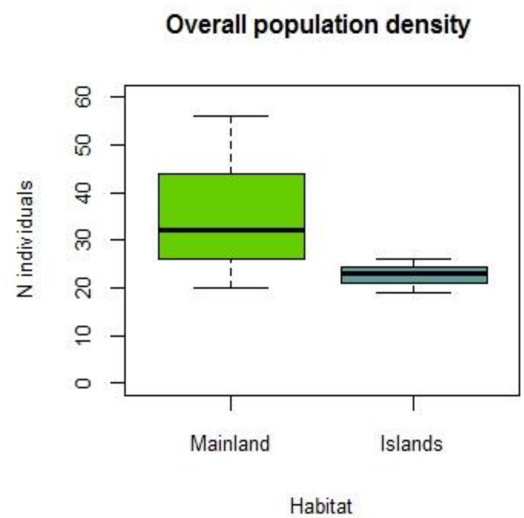


Figure 5.6 Boxplot representing the average values of overall population density calculated over the tree trapping sites on the mainland and on the islands. Values represent the Minimum Number Alive (MNA) of *A. agrarius*, *A. flavicollis* and *A. sylvaticus* trapped on the mainland and on the islands (N= 3sites on the mainland and N=3 sites on the islands). The bold line in the boxes represents the median. The median, the first and third quartile and 95% confidence interval of median are represented in each of the boxplots.

Table 5.3 Rank order of sites from both habitats according to densities of individuals (from highest to lowest) for *A. agrarius*, *A. flavicollis*, *A.sylvaticus* and for all three species combined.

Rank	***Ag***	***Af***	***As***	***Combined***
1	M2	M2	I2	M2
2	M1	I3	M1	I3
3	M3	M3	M2	M1
4	I2	I2	I1	I2
5	I1	M1	I3	M3
6	I3	I1	M3	I1

5.3.3 Food resources in the two habitats

The values of the three variables used as a proxy for resource availability, *percentage tree cover* (W=1595.5, p<0.01, N=48+48), *number of all shrubs* (W=1440, p=0.03, N=48+48) and *number of shrubs with seeds* (W=1595.5, p<0.01, N=48+48), were significantly higher on the mainland than on islands (Figure 5.7). Mean values of the variables describing resource availability calculated for each trapping site are reported in Table 5.1.

5.3.4 Distance of the centre of the home range from habitat edges

On average mainland animals had home ranges which were 25m±10 distant from the closest habitat edge, while island animals had home ranges which were 14m±9 distant from the closest habitat edge, the difference being significant (Welch Two Sample t-test: t=2.19, df=14.62, p=0.04; N=8 mainland, N=9 islands).

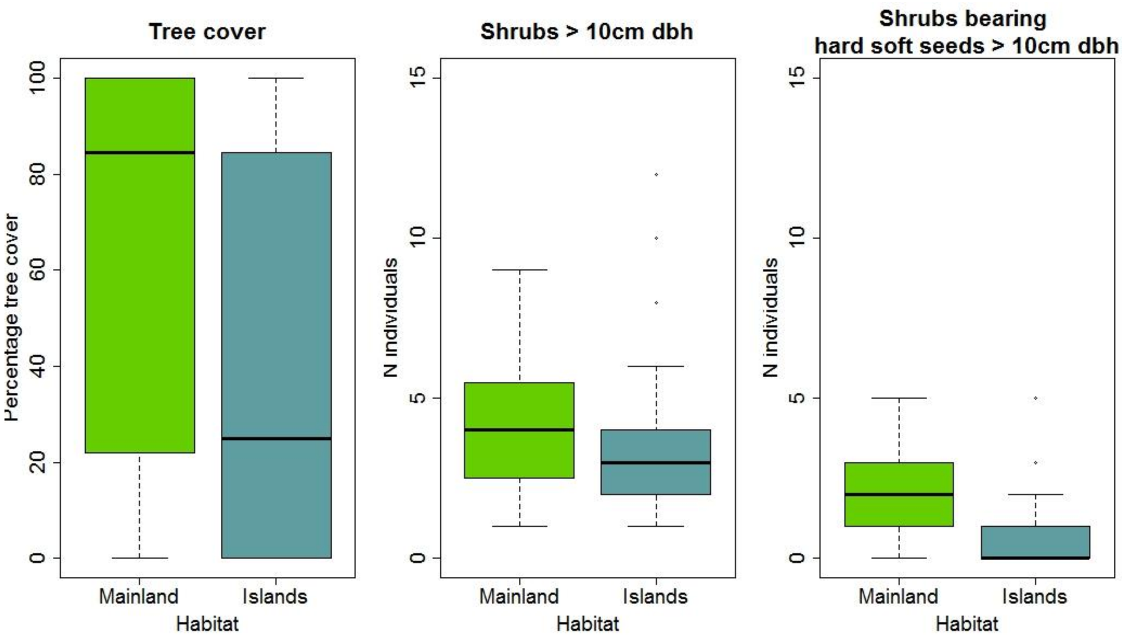


Figure 5.7 Box plots representing resource availability variables sampled on the mainland and on the islands. Tree cover=*percentage of tree cover*; Shrubs > 10cm dbh= *total number of shrub individuals > 10cm.* Shrubs bearing hard soft seeds >10cm dbh= *total number of shrub individuals carrying hard and soft seeds* counted in the trapping sites. N=48 mainland, N=48 islands. The median, the first and third quartile and 95% confidence interval of median are represented in each of the boxplots.

5.3.5 Factors affecting home range and core area size

Multiple linear regression analysis was used to develop two models for studying the relationship between home range/core area size and the three variables *overall population density*, *number of shrubs with seeds* and *minimum distance of the centre of the home range from edge habitat*. For both the models on home range and core area sizes, basic descriptive statistics and regression coefficients are shown in Table 5.4.

Only *number of number of shrubs with seeds* and *minimum distance of the centre of the home range from edge habitat* had a significant effect (p <0.01) on home range size. The model with the two significant predictors (the most parsimonious model) was able to account for 75% of the variance in home range size, $F_{(2, 14)}$ =23.89, p< 0.01. Also for core areas, *number of shrubs with seeds* and *minimum distance of the centre of the home range from edge habitat* had a significant effect (p<0.01) on their size. In this case, the most parsimonious model was able to account for 70% of the variance in core area size, $F_{(2, 14)} = 19.83$, p< 0.01. Home ranges and core areas decreased in size with increasing *minimum distance of the centre of the home ranges from habitat edges*, and with decreasing *number of shrubs with seeds* (Figures 5.8, 5.9, Table 5.4). *Overall population density* also showed a negative relationship with the sizes of home ranges and core areas, i.e. the higher the density, the smaller the home range and the core areas, but the relationships were not significant (Figures 5.8, 5.9, Table 5.4).

A further multiple regression analysis was run using *A. agrarius* density instead of overall population density. However, there was no model improvement and again the coefficient for density, besides being negative, was not significant; these results are not included. Values of Spearman correlations coefficients between home range size and the four independent variables are reported in Figures 5.8 and 5.9.

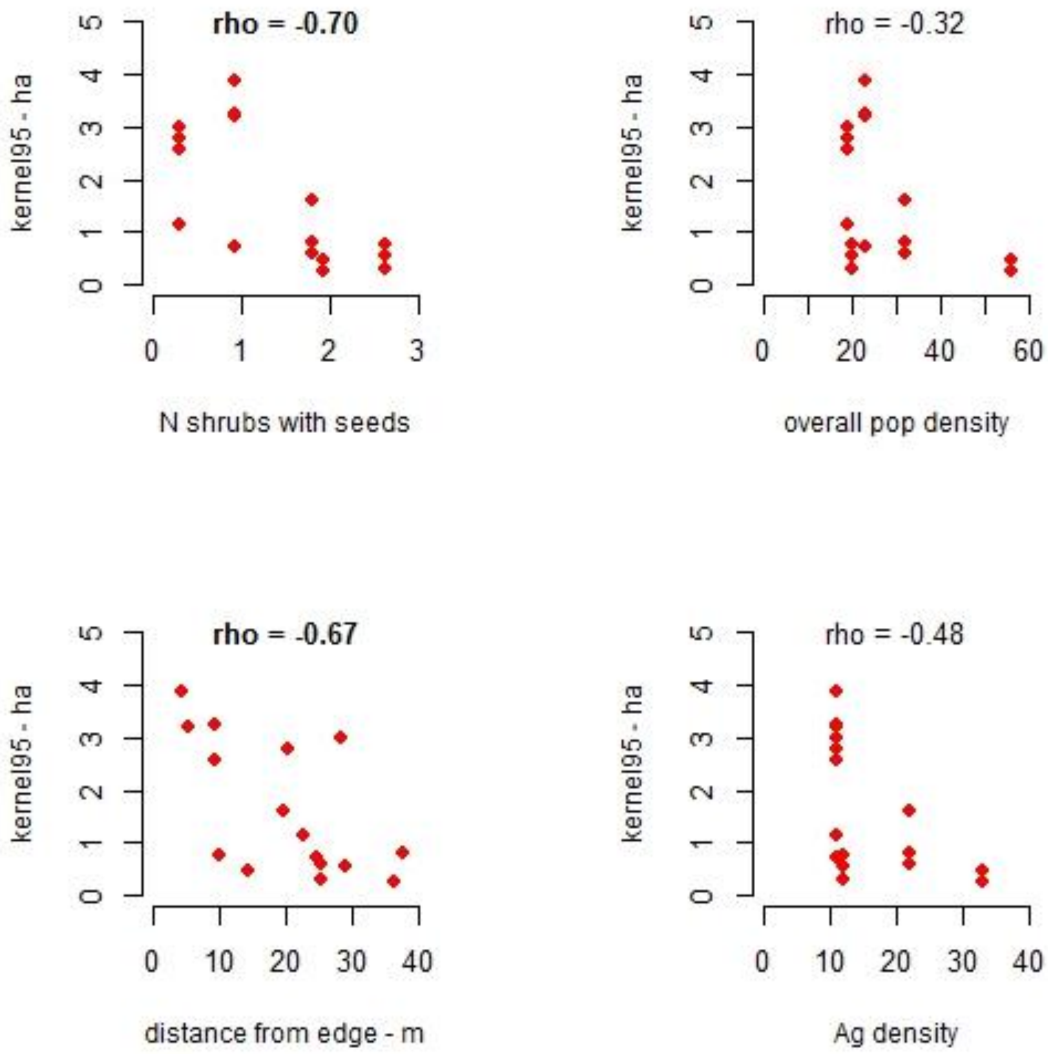


Figure 5.8 Relationship between home range size (kernel95 estimator, in hectares) and food resource variables (*N shrubs with seeds*), *overall population density (N individuals trapped in each grid), distance from the centre of the home range from the closest habitat edge* (in meters) and *A. agrarius density*. Values of the Spearman correlation coefficient between home range size and the independent variables are reported in each plot. Values in bold represent significant correlations.

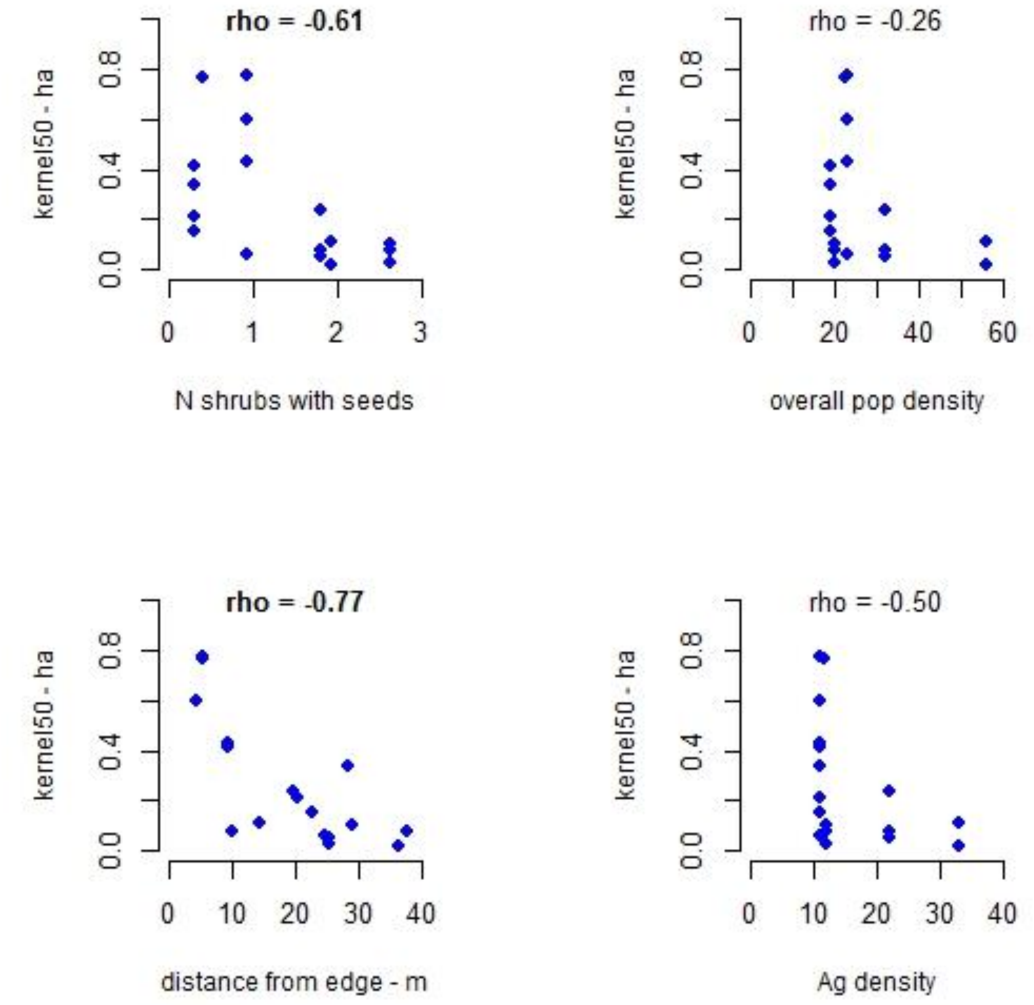


Figure 5.9 Relationship between home range size (kernel50 estimator, in hectares) and food resource variables (*N shrubs with seeds*), *overall population density (N individuals trapped in each grid), distance from the centre of the home range from the closest habitat edge* (in meters*)* and *A. agrarius density*. Values of the Spearman correlation coefficient between core area size and the independent variables are reported in each plot. Values in bold represent significant correlations.

Table 5.4 Results of linear regression models examining the effects of resource availability (i.e. N shrubs carrying seeds dbh >10), density of competitors (*overall pop density*) and of minimum distance of the centre of the home range from edge habitat (Distance from habitat edges) on the home range (HR) and core area (CA) size of male *A. agrarius. Results for full models and most parsimonious model are reported in the table.*

	Coefficient	***t***	***p***
HR size, n=17, Adjusted R^2=0.74 - full model - $F_{3,13}$=16.55, p<0.01			
Constant	12.29	10.88	0.00
Overall population density	-0.41	-1.09	0.29
Number of shrubs with seeds	-0.62	-4.07	0.00
Distance from habitat edges	-0.03	-3.09	0.00
HR size, n=17, Adjusted R^2=0.75 - most parsimonious model - $F_{2,14}$=23.89, p<0.01			
Constant	11.10	40.80	0.00
Number of shrubs with seeds	-0.04	-3.34	0.00
Distance from habitat edges	-0.67	-4.58	0.00

	Coefficient	***t***	***p***
CA size, n=17, Adjusted R^2=0. 68 - full model - $F_{3,13}$=12.45, p<0.01			
Constant	9.87	6.60	0.00
Overall population density	-0.18	-0.37	0.71
Number of shrubs with seeds	-0.61	-3.03	0.00
Distance from habitat edges	-0.06	-3.59	0.00
CA size, n=17, Adjusted R^2=0. 70 - most parsimonious model - $F_{2,14}$=19.83, p<0.01			
Constant	9.32	26.95	0.00
Number of shrubs with seeds	-0.63	0.19	0.00
Distance from habitat edges	-0.06	-3.85	0.00

5.4 Discussion

This study showed a significant difference in the characteristics of home ranges of male *A. agrarius* in the two main habitats of the dynamic floodplain of the River Tagliamento, with the size of home ranges and core areas on the mainland being significantly smaller than those on islands. The sizes of home ranges on the mainland (range 0.3-1.6 ha), were comparable to those of other *Apodemus* species measured through radio-tracking (e.g. Stradiotto et al. 2009; Tew and Macdonald 1994; Wolton 1985). On the islands, instead, home ranges were up to four times larger (range:0.7-5.4ha) than on the mainland (range:0.3-1.6ha) and hence larger than those of other *Apodemus* species. Comparable results were obtained for the core areas, which appeared to be up to five times larger on islands (range mainland: 0.1-0.2ha, range islands: 0.1-0.7ha). Size of core areas measured on the mainland in this study were comparable to values found by Stradiotto et al. (2009) for *A. flavicollis inhabiting* in a beech woodland in Italy.

5.4.1 Factors that affect home range size

Of the three factors considered as potentially influencing home range size, *overall population density*, *number of shrubs with seeds*, and *minimum distance of the centre of the home range from edge habitat*, only the latter two were significant. The fact that the density of competitors was not significant was rather unexpected as this is a factor that has often been found to negatively affect home range size of vertebrates (Lopez-Sepulcre and Kokko 2005; Schradin et al. 2010). In studies of small mammals in which neighbours were experimentally removed (red squirrel, *Tamiascurius hudsonicus* Boutin & Schweiger 1988; African striped mouse, *Rhabdomys pumilio* Schoepf et al. 2015), the remaining individuals enlarged their home ranges, showing that territorial interactions with neighbouring individuals constrain space use (Jetz et al. 2004).

In this study, the density of *Apodemus agrarius* was higher on the mainland than on the islands, supporting the trend found in chapter 4 which used a larger sample, as 10 islands overall were sampled. Also overall population density showed a decreasing trend moving from the mainland to the islands. Despite this, the regression analysis did not identify either *A. agrarius* density or overall population density as significant predictors explaining the observed variation in home range size. It is possible that the absence of a significant effect was due to the fact that there were only six measures of *A. agrarius* density and overall population density taken at a given point in time. Therefore it is possible that the sample size was too small to obtain statistically significant results in terms of differences in densities between mainland and island populations. Even though overall population density was not significant, the coefficient of the regression equation was negative, indicating that the relationship between size of home range size and population density was going in the expected direction, with smaller home ranges where densities were higher. The same argument can be used for explaining the lack of significant relationships between home range size and density of *A. agrarius.* Density of *A. agrarius* despite not resulting in a significant predictor in explaining variation in home range size through linear regression analysis showed a high value of Spearman correlation coefficient with home range size (rho=-0.48, p=0.06). Therefore it is not possible to exclude that density did have an effect on the size of home ranges of males *A. agrarius* in the Tagliamento floodplain but more likely that the sample size in this study did not have the power to detect this effect. However, a few studies investigating the spatial behaviour of small mammals did not observe a negative density dependent effect on home range size (e.g. Hoset et al. 2008, for *Microtus oeconomus*; Ostfeld 1986 for *M. californicanus*; Sera and Gaines 1994 for *M. ochrogaster*).

The abundance of food resources was however significantly related with the size of the home ranges, with greater abundance corresponding to smaller home ranges. Previous studies that discussed the spatial organization of oceanic island and mainland mammals reported smaller home ranges for island individuals in comparison to their mainland counterparts (e.g. Adler et al. 1997; Gliwicz 1980, 1989; Mazurkiewicz 1971). Sale and Anould (2009) compared the spatial behaviour of mainland and island populations of the insectivorous Swamp Antechinus (*Antechinus minimus maritimus*) in south-western Australia and found that the reduced home range size of island individuals is a direct consequence of increased food resources available on islands with respect to the mainland. Indeed, several studies showed how the most common explanation for inter-population differences in home range size of small mammals, relates to increased or decreased food abundance (Corp et al. 1997; Jones 1990a; Schradin and Pillay 2006; Stradiotto et al. 2009). Furthermore, it has been widely demonstrated that home ranges of small mammals supplemented with additional food in the wild generally become considerably smaller than those not supplemented (e.g. Ims 1987; Schoepf et al. 2015).

Results obtained in this chapter confirm the observation that home ranges are smaller where resources are higher. In this case, floodplain resources were higher on the mainland as opposed to islands. The trends in resource availability in the two habitats that emerged in this chapter confirm patterns already found in previous chapters of this thesis obtained through different sampling, namely that the mainland is characterized by higher availability and diversity of trees and seed bearing shrub species (Figure 4.6 in chapter 4 and Figure 5.7 in the present chapter). Furthermore, the spatial configuration of the habitats of the Tagliamento floodplain was likely to be determinant in explaining the observed variation in home range size for the males of *A. agrarius*. The spatial allocation of food resources on the islands of the floodplain is patchy, while on the mainland it is continuous. Therefore on the mainland resources are not only more abundant per unit area, but they are also continuously distributed while on the islands they are interspersed by matrix habitat (gravel) that bears no resources. As discussed in other studies examining the spatial behaviour of small mammals in continuous versus patchy or fragmented habitats, the fact that food resources are not continuously distributed, can have large impact on the home range size of the individuals, which have to move more to find enough food to satisfy their ecological daily needs (Bowers et al. 1996; Collins et al. 1997; Diffendorfer et al. 1995).

Finally, the results of the liner regression highlighted edge effects as a potential factor linked to home range size. Mice inhabiting the river islands of the Tagliamento tended to live significantly closer to habitat edges than mainland mice and a negative relationship between the minimum distance of the centre of the home range from habitat edges and home range size was found. Animals whose centre of the home range was more distant from habitat edges had smaller home ranges than animals that had this centre closer to habitat edges. Stamps et al. (1987) observed that the home range of animals living in patchy habitats is larger than the home range of animals living in continuous habitats, given that the former are usually characterized by high percentages of edge habitat. The authors discussed this phenomenon on the basis of lower intruder pressure in patchy habitats: i.e. in patchy habitats lower densities of conspecifics and competitors are usually found at the edges than in interior habitats, therefore determining a negative density dependent increase in the size of the home range of those individuals living close to edges.

The present radio-tracking study on *A. agrarius* lacks a comparison between density of animals at island or mainland edges and animals living in the interiors of these two habitats. Therefore the increase in home range size for those animals living close to edges cannot be explained through the hypothesis of a lower intruder pressure at habitat edges. However, a possible explanation for the differences in the spatial behaviour of mainland/island animals could be found in the configuration of the Tagliamento floodplain and in the type of edge that mice have to cross when moving within their home range. Mostly all the animals living on islands had home ranges and core areas encompassing also the matrix of gravel surrounding the islands (and therefore the edge between gravel and riparian woodland, Figure 5.3), while on the mainland just three out of the eight animals tracked had home ranges which incorporated edges (animal 628 on M2 and 514 on M1 and animal 575 on M3 which showed the external borders of their home ranges placed against to a big water channel or a big agricultural field). This could be due to the fact that animals living on the mainland (especially at sites M1 and M2) had a deep channel of water adjacent to the riparian forest acting as a potential deterrent for dispersion into the active tract. Conversely, animals living at island sites were able to incorporate the gravel matrix surrounding the islands in their home ranges (and often also in the core areas), without encountering a water channel. Thus mice must have been aware of the presence of edges with different permeability. Animals living on islands which moved through the surrounding open gravel matrix, incorporated in their home ranges the gravel matrix itself, small pioneer islands and uprooted trees deposited on gravel bars. In this sense the edge dividing the mainland from the active tract, being characterized by the presence of a deep water channel, can be seen as an impermeable edge for *A. agrarius,* while the edge between island and gravel matrix can be seen as a permeable one (sensu Stamps et al. 1985), which males of the species cross in their daily movements thus affecting the magnitude of their movements and consequently increasing the size of their home ranges.

5.4.2 Factors that affect core area size, number and distance

Core areas are parts of an animal's home range that are intensively used and in several studies on *Apodemus* spp. nests were often located inside them (Rosalino et al. 2011a; Stradiotto et al. 2009; Wolton 1985). Up to the present study there was no information about the size of core areas and distance between core areas for *A. agrarius*. Stradiotto et al. (2009), found that males of *A. flavicollis* used several core areas within their home ranges in woodlands of north-eastern Italian Alps and they suggested that this behaviour could decrease the risk of predation, by reducing the time required to return to a nest.

Males and females of *Apodemus* species are known to use several nests, especially during the breeding season and to move them within their range (Rosalino et al. 2011a; Wolton 1983; Wolton and Flowerdew 1985). Wolton (1983) found that a radio-tracked male of *A. sylvaticus* in deciduous woodland of NE Scotland, used as many as four nests within 15 days. The author suggested that the changes in the position of nests could be due to interactions with conspecifics and predators. *Apodemus* spp. have also been shown to select areas with great protection for nest placement, reducing predation risk associated with social or food consumption behaviour in the vicinity of nest sites (under thick vegetation, on steep slopes and far from any sort of human or environmental perturbation or between the roots of trees) (Babinska-Werka et al. 1979 for *A. agrarius*; Rosalino et al. 2011 for *A. sylvaticus*;

Stradiotto et al. 2009 for *A. flavicollis*). In the present study, nests of *A. agrarius* were not located; it can be predicted that, as a response to an increased size of home ranges on islands, they should have more nest sites and more core areas, but the latter was not found. This was something not expected, given the high predation risk associated with crossing habitats like the gravel matrix or on the islands themselves, where the vegetation cover is in general lower than on the mainland (see individuals 591 and 611 in Figure 5.3).

The regression analysis suggests that the variability in core area size is likely to be due, as for home range size, to the variability in resource availability, with fewer resources requiring larger core areas to satisfy energetic needs. It is possible that the number of core areas on islands was not higher, despite larger home ranges, because of the lower availability on islands of suitable nest locations. Islands are themselves patchy in their vegetation structure, being characterised by areas with thick over-storey and under-storey vegetation alternating with more open areas without thick shrubs or trees and just rarefied grasses as ground cover. Whereas the mainland, where core areas were closer to each other, is more continuous and constant in its vegetation structure, being characterised by thick over-storey and under-storey levels and dense ground cover almost everywhere.

5.4.3 Conclusions

This study is limited to males of *A. agrarius* only during a particular season and data have been collected over a single year, however this is the first study of the home range characteristics of *A. agrarius* carried out by means of radio-tracking. Previous studies have been conducted on the spatial behaviour of *A. agrarius* employing methods that allow for less accurate home range estimates such as trapping and colour baits (Liro and Szacki 1987; Vukicevic-Radi et al. 2006). The value of this study lies in the fact that it compares the home ranges of individuals of *A. agrarius* living in two different habitats at the same point in time. Even though animals were tracked for a relatively short time (ten days) the differences between home ranges in these two habitats were very evident and significant and likely attributable to resource abundance and habitat edge effects. It is also likely that the presence of competitors (*A. flavicollis* and *A. sylvaticus*) and of conspecifics had an impact on the size of home ranges and core areas, but the number of measurements was probably too small to detect this effect.

Spatial organization of males in small mammals was described to be driven also by the distribution and density of females coming into oestrus (Waterman 2007): therefore it was also possible that the detected differences in the spatial behaviour of *A. agrarius* between the mainland and the islands was affected partly also by a lower density of reproductive females on the islands, as already observed in other woodland habitats (e.g. Ostfeld et al. 1996), due to a lower density of reproductive females (as emerged in Chapter 4, Figure 4.3, section 4.3.1) or to a delayed females' oestrus on islands, something which has proved to happen on oceanic islands (Salvador and Fernandez 2008 for *Cavia intermedia* in southern Brazil).

This study has confirmed what many other studies of home ranges have found, namely that that the characteristics of the habitat and the distribution and density of resources have a large effect on the distances animals have to travel and hence on their survival effort. This study also suggests that the island environment of the Tagliamento floodplain is a less desirable habitat for *A. agrarius* than the mainland habitat, as it requires greater expenditure of energy by requiring the animals to move greater distances to acquire sufficient resources.

5.5 References

Adler, G.H., Endries, M., Piotter, S., 1997. Spacing patterns within populations of a tropical forest rodent, Proechimys semispinousus, on five Panamanian islands. Journal of Zoology 241, 43-53.

Arthur, S.M., Manly, B.F.J., McDonald, L.L., Garner, G.W., 1996. Assessing habitat selection when availability changes. Ecology 77, 215-227.

Babinska-Werka, J., Gliwicz, J., Goszczynski, J., 1979. Synurbization processes in a population of *A. agrarius*. Habitats of the Striped Field Mouse in town. Acta Theriologica 24, 405-415.

Barreto, G.R. and MacDonald, D.W., 2000. The decline and local extinction of a population of water voles, Arvicola terrestris, in southern England. Zeitschrift fur Saugetierkunde 65, 110-120.

Bond, M.L. and Wolff, J.O., 1999. Does Access to Females or Competition among Males Limit Male Home-Range Size in a Promiscuous Rodent? Journal of Mammalogy 80, 1243-1250.

Boutin, S., and Schweiger, S., 1988. Manipulation of intruder pressure in red squirrels (*Tamiasciurus hudsonicus*): effects on territory size and acquisition. Canadian Journal of Zoology 66, 2270-2274.

Boutin, S., Wauters, L.A., McAdam, A.G., Humphries, M.M., Tosi, G., Dhondt, A.A., 2006. Anticipatory reproduction and population growth in seed predators. Science 314, 1928-1930.

Bowers, M.A., Welch, D.N., Carr, T.G., 1990. Home range size adjustments by the eastern chipmunk, Tamias striatus, in response to natural and manipulated water availability. Canadian Journal of Zoology 68, 2016-2020.

Bowers, M., Gregario, K., Brame, C.J., Matter, S.F., Dooley, J.L., 1996. Use of space and habitat by meadow voles at the home range, patch and landscape scales. Oecologia 105, 107-115.

Boutin, S., 1990. Food supplementation experiments with terrestrial vertebrates: patterns problems, and the future. Canadian Journal of Zoology 68, 203-220.

Burt, W.H., 1943. Territoriality and home range concepts as applied to mammals. Journal of Mammalogy 24, 346-352.

Collinge, S.K., 2009. Fragment context and edge effect, In Ecology of fragmented landscapes. ed. S.K. Collinge. John Hopkins University Press, Baltymore, Maryland.

Collins, R.J. and Barret, G.W., 1997. Effects of habitat fragmentation on meadow vole (Microtus pennsylvanicus) population dynamics in experiment landscape patches. Landscape Ecology 12, 63-76.

Constible, J.M., Chamberlain, M.J., Leopold, B.D., 2006. Relationships between landscape pattern and space use of three mammalian carnivores in central Mississippi. American Midland Naturalist 155, 352-362.

Corp, N., Gorman, M.L., Speakman, J.R., 1997. Ranging behaviour and time budgets of male wood mice Apodemus sylvaticus in different habitats and seasons. Oecologia 109, 242-250.

Diffendorfer, J.E., Gaines, M., Holt, R.D., 1995. Habitat fragmentation and movements of three small mammmals. Ecology 76, 827-839.

ESRI, 1992. ArcView GIS 3.2, Redlands, California, USA.

Falls, J.B., Falls, E.A., Fryxell, J.M., 2007. Fluctuations of deer mice in Ontario in relation to seed crop. Ecological Monographs 77, 19-32.

Forman, R.T.T. and Godron, M., 1981. Patches and structural components for a landscape ecology. BioScience 31, 733-740.

Gliwicz, J., 1980. Island populations of rodents - their organization and functioning. Biological Reviews of the Cambridge Philosophical Society 55, 109-138.

Gliwicz, J., 1981. Competitive interactions within a forest rodent community in central Poland. Oikos 37, 353-362.

Gliwicz, J., 1989. Individuals and populations of the bank vole in optimal, suboptimal and insular habitats. Journal of Animal Ecology 58, 237-247.

Gurnell, J. and Flowerdew, J.R., 2006. Live trapping small mammals. A practical guide, 4th edition Mammal Society, London, UK.

Harrington, G.N., Freeman, A.N.D., Crome, F.H.J., 2001. The effects of fragmentation of an Australian tropical rain forest on populations and assemblages of small mammals. Journal of Tropical Ecology 17, 225-240.

Harris, S., Cresswell, W.J., Forde, P.G., Trewhella, W.J., Woollard, T., Wray, S., 1990. Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. Mammal Review 20, 97-123.

Hayes, L. D., Chesh, A., Ebensperger, L. A., 2007. Ecological predictors of range areas and use of burrow systems in the diurnal rodent, Octodon degus. Ethology 113, 155–165

Hodder, K.H., Kenward, R.E., Walls, S.S., Clarke, R.T., 1998. Estimating core ranges: a comparison of techniques using the common buzzard (Buteo buteo). Journal of Raptor Research 32, 82-89.

Holisova, V., 1967. The food of Apodemus agrarius (Pall.). Zool. Listy 16, 1-14.

Hoset, K.S., Galliard, J.-F.L., Gundersen, G., Steen, H., 2008. Home range size and overlap in female root voles: Effects of season and density. Behavioral Ecology 19, 139-145.

Hovland, N., Andreassen, H.P., Ims, R.A., 1999. Foranging behaviour of the root vole Microtus oeconomus in fragmented habitats. Oecologia 121, 236-244.

Ims, R.A., 1987. Responses in spatial organization and behaviour to manipulations of the food resource in the vole Chlethrionomys rufocanus. Journal of Animal Ecology 56, 585-596.

Jetz, W., Carbone, C., Fulford, J., and Brown, J.H., 2004. The scaling of animal space use. Science 306, 266-268.

Jones, E.N., 1990a. Effects of forage availability on home range and population density of Microtus pennsylvanicus. Journal of Mammalogy 71, 382-389.

Kernohan, B.J., Gitzen, R.A., Millspaugh, J.J., 2001. Analysis of animal space use and movements., In Radiotracking and animal populations. eds J.J. Millspaugh, J.M. Marzluff. Academic Press, London, United Kingdom.

Krebs, C.J., 1999. Ecological methodology. Addison-Wesley Educational Publishers, Inc.

Krebs, J.R., 1971. Territory and breeding density in the great tit, Parus major L. Ecology 52, 1-22.

Kryštufek, S., 1991. Sesalci Slovenije. Prirodoslovni muzej Slovenije. Ljuljana, 294 pp.

Liro, A. and Szacki, J., 1987. Movements of the field mice Apodemus agrarius (Pallas) in a suburban mosaic of habitats. Oecologia 74, 438-440.

Lopez-Sepulcre, A. and Kokko, H., 2005. Territorial defense, territory size, and population regulation. American Naturalist 166, 317-329.

Mares, M.A. and Lacher, T.E., 1987. Social spacing in small mammals: patterns of individual variation. American Zoologist 27, 293-306.

Mares, M. A., Lacher, T. E. jr, Willig, M.R. and Bitar, N. A., 1982. An experimental analysis of social spacing in *Tamias striatus*. Ecology 63, 267–273.

Mayeikyte, R., 2002. Small mammals in the mosaic landscape of Eastern Lithuania: species composition, distribution and abundance. Acta Zoologica Lituanica 12, 381-391.

Mazurkiewicz, M., 1971. Shape, size and distribution of home ranges of Chlethrionomys glareoulus (Schreber, 1780). Acta Theriologica 16, 23-60,

Merrit, J.F., Lima,M., Bozinovic, F., 2001. Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. Oikos 94, 505-514.

Morris, G., Conner, L.M., Oli, M.K., 2011. Effects of mammalian predator exclusion and supplemental feeding on space use by hispid cotton rats. Journal of Mammalogy 92, 583-589.

O'Neill, R.V., Milne, B.T., Turner, M.G., Gardner, R.H., 1988. resource utilization scales and landscape patterns. Landscape Ecology 2, 63-69.

Ostfeld, R.S., Jones, C.G., Wolff, J.O., 1996. Of mice and mast: ecological connections in eastern deciduous forests. BioScience 46, 323-330.

Ostfeld, R.S., 1986. Territoriality and mating system of California voles. Journal of Animal Ecology 55, 691-706.

Otis, D.L. and White, G.C., 1999. Autocorrelation of location estimates and the analysis of radiotracking data. Journal of Wildlife Management 63, 1039-1044.

Raska-Jurgiel, E., 2001. Movement behaviour of woodland rodents: looking from beyond small trapping grids. Acta Theriologica 46, 145-159.

Relyea, R.A., Lawrence, R.K., Demarais, S., 2000. Home range of a desert mule deer: testing body size and habitat productivity hypothesis. Journal of Wildlife Management 64, 146-153.

Ribble, D.O., Wurtz, A.E., McConnell, E.K., Buegge, J.J., Welch, K.C., Jr., 2002. A Comparison of Home Ranges of Two Species of Peromyscus Using Trapping and Radiotelemetry Data. Journal of Mammalogy 83, 260-266.

Rooney, S., Wolfe, A., Hayden, T.J., 1998. Autocorrelated data in telemetry studies: time to independence and the proble of behavioural effects. Mammal Review 28, 89-98.

Rosalino, L.M., Ferreira, D., Leitão, I., Santos-Reis, M., 2011a. Selection of nest sites by wood mice Apodemus sylvaticus in a Mediterranean agro-forest landscape. Ecological Research 26, 445-452.

Rosalino, L.M., Ferreira, D., Leitão, I., Santos-Reis, M., 2011b. Usage patterns of Mediterranean agro-forest habitat components by wood mice Apodemus sylvaticus. Mammalian Biology 76, 268-273.

R Team, R.D.C., 2012. R: A language and environment for statistical computing, ed. R.F.f.S. Computing, Vienna, Austria.

Sale, M.G. and Arnould, J.P.Y., 2009. Spatial and temporal organization in the swamp antechinus: comparison between island and mainland populations. Journal of Mammalogy 90, 347-355.

Šálek, M., Drahníková, L., Tkadlec, E., 2015. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. Mammal Review 45, 1-14.

Salvador, C.H. and Fernandez, F.A.S., 2008. Reproduction and growth of a rare, island endemic cavy (Cavia intermedia) from southern Brazil. Journal of Mammalogy 89, 909-915.

Schnitzler, A., 1997. River dynamics as a forest process: Interaction between fluvial systems and alluvial forests in large European river plains. The Botanical Review 63, 40-64.

Schoepf, I., Schmohl, G., König, B., Pillay, N., Schradin, C., 2015. Manipulation of population density and food availability affects home range sizes of African striped mouse females. Animal Behaviour 99, 53-60.

Schradin, C. and Pillay, N., 2006. Female striped mice (Rhabdomys pumilio) chenage their home ranges in response to seasonal variation in food availability. Behavioural Ecology 17, 452-458.

Schradin, C., Schmol, G., Rodel, H.G., Treffer, S.M., Brenner, J., Pillay, N., 2010. Female home range size is regulated by resource distribution and intraspecific competition: a long term field study. Animal Behaviour 79, 195-203.

Selonen, V., Hanski, I.K., Stevens, P.C., 2001. Space use of the Siberian flying squirrel Pteromys volands in fragmented forest landscapes. Ecography 24, 588-600.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., Swift, D.M., 1987. Large Herbivore Foraging and Ecological Hierarchies. BioScience 37, 789-799.

Sera, W.E. and Gaines, M.S., 1994. The effect of relatedness on spacing behavior and fitness of female prairie voles. Ecology 75, 1560-1566.

Siffczyk, C., Brotons, L., Kangas, K., Orell, M., 2003. Home range size of willow tits: a response to winter habitat loss. Oecologia 136, 635-642.

Sunde, P. and Redpath, S.M., 2006. Combining information from range use and habitat selection: sex-specific spatial responses to habitat fragmentation in a tawny owls Strix aluco. Ecography 29, 152-158.

Stamps, J.A. and Buechner, M., 1985. The territorial defense hypothesis and the ecology of insular vertebrates The Quartely Review of Biology 60, 155-181.

Stamps, J.A., Buechner, M., Krishnan, V.V., 1987. The effects of habitat geometry on territorial defense costs: intruder pressure in bounded habitats. American Zoologist 27, 307-325.

Stradiotto, A., Cagnacci, F., Delahay, R., Tioli, S., Nieder, L., Rizzoli, A., 2009. Spatial organization of the yellow-necked mouse: Effects of density and resource availability. Journal of Mammalogy 90, 704-714.

Szacki, J. and Liro, A., 1991. Movements of small mammals in the heterogeneous landscape. Landscape Ecology 5, 219- 224.

Tattersall, F.H., Macdonald, D.W., Hart, B.J., Manley, W.J., Feber, R.E., 2001. Habitat use by wood mice (Apodemus sylvaticus) in a changeable arable landscape. Journal of Zoology 255, 487-494.

R Developmental Core Team, 2012. R: A language and environment for statistical computing, ed. R.F.f.S. Computing, Vienna, Austria.

Tertil, R., 1972. The effect of behavioural thermoregulation on the daily metabolism of Apodemus agrarius. Acta Theriologica 22, 328-332.

Tew, T.E. and Macdonald, D.W., 1994. Dynamics of space use and male vigour amongst wood mice, Apodemus sylvaticus, in the cereal ecosystems. Behav. Ecol. Sociobiol. 34, 337-345.

Tucker, M.A., Ord, T.J., Rogers, T.L., 2014. Evolutionary predictors of mammalian home range size: Body mass, diet and the environment. Global Ecology and Biogeography 23, 1105-1114.

Tufto, H., Andersen, R., Linnel, J., 1996. Habitat use and ecological correlates of home range size in a small cervid: the roe deer. Journal of Animal Ecology 65, 715-724.

Vukicevic-Radi, O., Mati, R., Kataranovski, D., Stamenkovi, S., 2006. Spatial organization and home range of Apodemus flavicollis and A. agrarius on Mt. Avala, Serbia. Acta Zoologica Academiae Scientiarum Hungaricae 52, 81-96.

Waterman, J., 2007. Male mating strategies in rodents, In Rodent Societies, an ecological and evolutionary perspective. eds J.O. Wolff, P.W. Sherman, p. 610. University of Chicago Press, Chicago and London.

Wauters, L. and Dhondt, A.A., 1992. Spacing behaviour of red squirrels, Sciurus vulgaris: variation between habitats and the sexes. Animal Behaviour 43, 297-311.

Wauters, L.A., Matthysen, E., Adriaensen, F., Tosi, G., 2004. Within density dependence and population dynamics of red squirrels *Sciurus vulgaris*. Journal of Animal Ecology 73, 11-25.

Wolff, J.O., 1985. The effects of density, food, and interspecific interference on home range size in Peromyscus leucopus and Peromyscus maniculatus. Canadian Journal of Zoology 63, 2657-2662.

Wolff, J.O., 1993. Why are female small mammals territorial? Oikos 68, 364-370.

Wolton, R.J., 1983. The activity of free-ranging wood mice Apodemus sylvaticus. Journal of Animal Ecology 52, 781-794.

Wolton, R.J., 1985. The ranging and nesting behaviour of Wood mice, Apodemus sylvaticus (Rodentia:Muridae), as revealed by radio-tracking. Journal of Zoology 206, 203-224.

Wolton, R.J. and Flowerdew, J.R., 1985. Spatial distribution and movements of woodmice, yellow-necked mouse and bank voles. Symposia of the Zoological Society of London 55, 249-275.

Wolton, R.J. and Trowbridge, B.J., 1985. The effects of radio-collars on Wood mice, Apodemus sylvaticus. Journal of Zoology 206, 222-224.

Ylonen, H., Altner, H.J., Stubbe, M., 1991. Seasonal dynamics of small mammals in an isolated woodlot and its agricultural surroundings. Annales Zoologici Fennici 28, 7-14.

Yunger, J.A., 2004. Movement and spatial organization of small mammals following vertebrate predator exclusion. Oecologia 139, 647-654.

Appendix 5.1

Animal ID, habitat where it was trapped and radio-tracked, home range (kernel 95), core area (kernerl 50) size in hectares, Minimum Convex Polygon (MCP, area, in hectares) used to calculate home range overlap, number of core areas (NCA) and number of fixes taken for each individual and used to estimate home range size. Just values for animals that showed an asymptotic curve in a plot of the cumulative number of days versus home range size are reported in the table and were used to run all the analysis.

ID	***Habitat***	***Kernel95*** *(ha)*	***Kernel50*** *(ha)*	***NCA***	***N fixes***
485	M1	0.8	0.08	1	34
514	M1	1.6	0.24	3	36
CM	M1	0.6	0.04	2	32
642	M2	0.5	0.11	3	47
628	M2	0.3	0.02	1	30
1024	M3	0.3	0.02	1	46
560	M3	0.7	0.07	1	39
575	M3	0.5	0.10	2	42
611	I2	5.4	0.76	1	41
590	I1	3.0	0.34	3	30
591	I1	2.5	0.41	3	25
594	I1	1.1	0.15	1	29
600	I1	2.8	0.21	1	31
564	I3	0.7	0.06	1	48
566	I3	3.2	0.77	2	48
568	I3	3.8	0.60	3	47
569	I3	3.2	0.43	2	46

Chapter 6 - Habitat use of the stone marten (*Martes foina*) in a natural riparian landscape

Abstract

Studies of patch use by carnivores in fragmented landscapes highlight the importance of the spatial context and the amount of food resources. Such studies have, however, never been carried out in a natural riparian floodplain characterized by the presence of river islands. This chapter reports the results of an exploratory analysis aimed at investigating the presence of carnivores on the mainland and the islands and the role of food resources and the spatial context in determining habitat use by the stone marten (*Martes foina*) on the riparian floodplain of the River Tagliamento.

The presence of *M. foina* and *Vulpes vulpes*, the two most common carnivores in the area, was determined at 18 sites (two mainland sites and 16 islands) by means of scent stations with camera traps and track surveys during the course of four seasons. Only *M. foina* was analysed for habitat use, as *V. vulpes* was nearly ubiquitous. *M. foina* tracks were found mostly in autumn, representing most likely dispersing juveniles, and presence/absence data for this season were analysed through logistic regression in relation to the following variables: area of the site, distance of each site from the mainland, site neighbourhood (a variable considering the spatial proximity between sites) and food abundance (fruits and small mammals).

The best model indicated that fruit abundance significantly contributed to determine the use of natural riparian mainland and island sites by *M. foina*. The model highlighted also a trend for the species to avoid the smallest and most isolated islands in the floodplain.

Results are discussed in the context of previous findings of habitat use of *M. foina* in Mediterranean riparian corridors, of the factors that could have affected data collection and in view of their consequences in projects of river restoration in Europe.

6.1 Introduction

Riparian corridors provide prime wildlife habitats characterized by the presence of food, shelter, and water for a variety of animal species (Naiman et al. 1993). They are important for maintaining landscape connectivity and biological connections for wildlife (Clerici and Vogt 2013). River mosaics include water channels, gravel bars, and shorelines that function as habitat for some species of amphibians and insects (Indermaur et al. 2009; Rust 1998) and in naturally conserved rivers river mosaics include also river islands (Tockner et al. 2003). In the United States, the use of natural and semi-natural rivers characterized by the presence of river islands has been investigated for mammalian carnivores. These studies highlighted that river islands are in general less used by mammalian carnivores, indeed river islands have been long recognized for their value to ground-nesting waterfowls because of the reduced predation (Duebbert et al. 1983; Hammond and Mann 1956). The use of river islands by carnivores has been shown to be site-specific (islands found in the upper and middle segments were visited more frequently than islands found in segments close to the mouth of the river), seasonal (more frequent use in some periods of the year when river flow is slower) (Zoellick et al. 2005) and dependent on local factors such as alternate prey availability (Crabtree and Wolfe 1988) or size and isolation of the islands (Sovada et al. 1995). In Europe studies investigating the carnivores' use of river islands are lacking.

Use or non-use of a given species of different habitats helps us understand their response to landscape structure (Crooks 2002; Mortelliti et al. 2009; Mortelliti and Boitani 2008), given that species generally express their perception of the landscape and its attributes by their habitat use patterns (Wiens 1989). Habitat specialists exhibit a behaviour that shows high dependence on particular resources and strong sensitivity to habitat changes and habitat loss. On the other hand, habitat generalists are very plastic, able to survive in many different habitats (e.g. Gentili et al. 2014; Haapakoski et al. 2013).

This chapter presents an exploratory analysis aimed at identifying the distributional pattern of *Martes foina* and *Vulpes vulpes* and, for *M. foina* only, the variables influencing use and non-use of the mainland and island sites present on the riverine mosaic of the Tagliamento. This analysis was carried out in order to understand the influence of food resources on carnivore use of the mainland and island sites of the riverine mosaic, with the aim to evaluate if food availability can overcome structural constraints on use of a given landscape element. In the particular mainland-island system of the Tagliamento and within the context of the central question of this thesis, this information can also provide an insight into the level of predator pressure exerted by carnivore species on the small mammal populations inhabiting the riverine islands of the Tagliamento.

The stone marten (*M. foina*) is a carnivore species that is very common in Mediterranean Europe landscape mosaics (Rondinini and Boitani 2002). It is a species typical of forested and rural habitats (Virgos and Garcia 2002), but it occurs rather frequently also in Mediterranean and Alpine riparian habitats (Prigioni et al. 2008; Santos 2010; Santos et al. 2011). It is a generalist predator, using a wide range of resources according to their local and seasonal availability (Genovesi et al. 1996).

Given the patchy nature of the Tagliamento floodplain, the study of how *M. foina* uses the mainland and island sites of the Tagliamento was investigated by applying the approach used in landscape ecology. The pattern of mainland and island sites use by the species was studied in relation to site size, isolation and also to variables describing food resources abundance. Use or non-use patterns of mammalian carnivores in fragmented landscapes have been investigated by various authors (e.g. Crooks and Soulè 1999; Swihart et al. 2003). This studies showed that the probability of patch use decreases with increasing patch isolation and decreasing patch size (Crooks 2002; Virgos and Garcia 2002), but it is also affected by the relative abundance of food resources in that patch (e.g. Mortelliti and Boitani 2008; Paquet et al. 2006).

In the system under study, it was predicted that the use *M. foina* makes of the habitats present in the Tagliamento floodplain could reflect a balance between the costs of reaching a given site (i.e. an island in the floodplain or a mainland site) and the benefit of finding enough resources in that site (Zollner and Lima 2005). Giving up on a given habitat and moving to another imposes energetic costs (Stephens and Krebs 1986) and increases predation risk (Zabala et al. 2003). Impaired foraging resulting from spatial isolation of food resources has been observed in frugivorous birds: visitation rates of fruit trees decreased with their isolation (Luck and Daily 2003). In this study, it was therefore predicted that an increase in food abundance would increase the probability of use of the large and easy to reach habitats like large islands or mainland sites, while it would not make a difference in the use of the spatially constrained habitats (e.g. islands which are isolated in the floodplain or very distant from the mainland).

6.2 Methods

6.2.1 Study area

Fieldwork took place on 16 islands and in two continuous areas of the adjacent mainland (called mainland sites MNLD1 and MNLD2 *hereafter*), for a total of 18 sampled sites (Figure 6.1). For a detailed description of the study area and of the different stages of development of islands, see Chapter 2, section 2.2.

Islands varied in size (range: 0.09–4.17ha, mean=1.03 ha±1.00), distance to mainland (range: 25-311m, mean=142 m ±97) and spatial proximity between them (proximity index within 1000m from each island edge: range 37.94-39.25, mean=38.49±0.49). Given the small size of the investigated islands relatively to the home range sizes of the target species, it is likely that individuals incorporated more than one island in their home range (Genovesi et al. 1997). Islands I2, I3, I4 (small islands) (Table 2.1 in Chapter 2, section 2.2) were not considered in this chapter. Mainland sites had an area >20ha and were quite close to each other (maximum distance=100m), but a fast flowing tributary of the Tagliamento (River Arzino), with a depth higher than one meter for most part of the year, separates the two sites. The River Arzino was considered as a barrier for the species, mainly because of the high speed of the stream before the confluence with the Tagliamento (Figure 6.1).

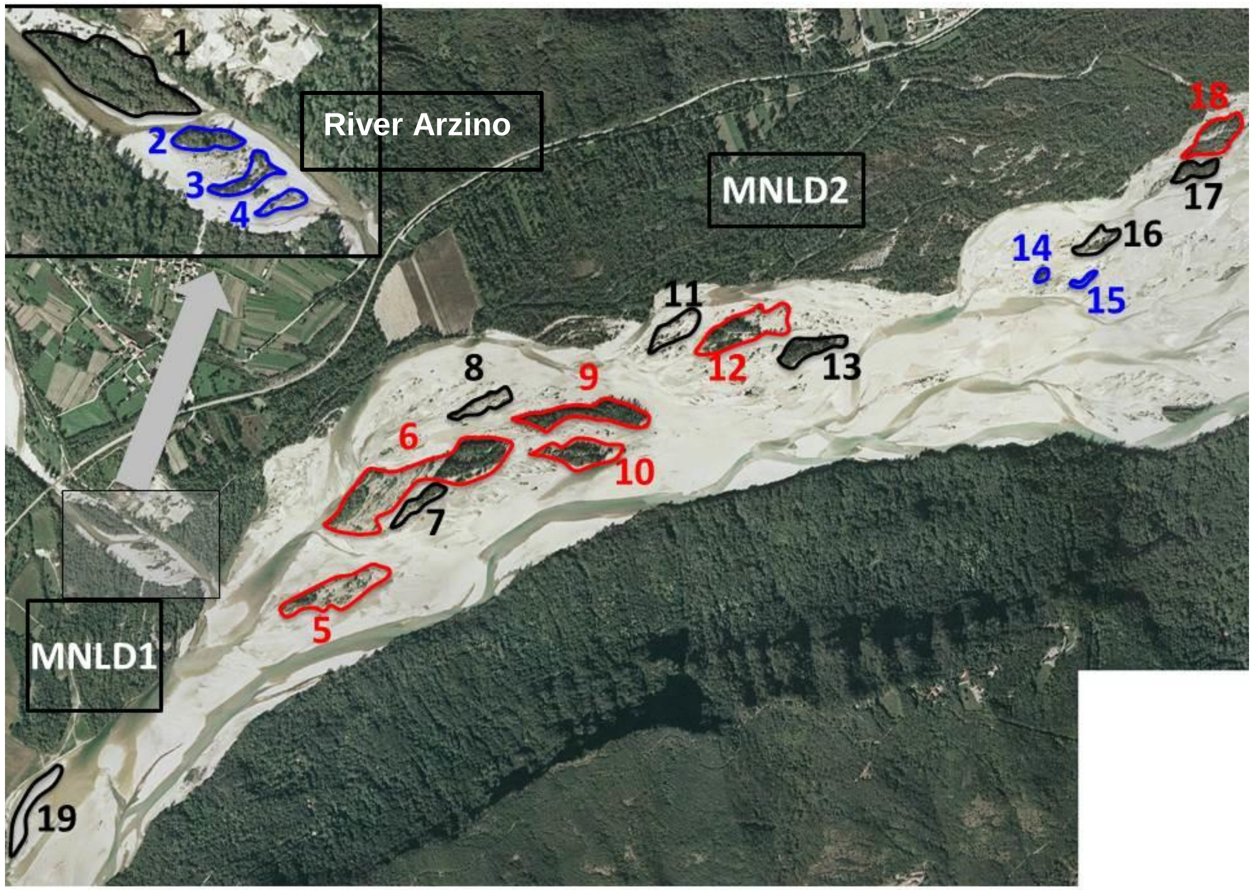


Figure 6.3 Location of the two mainland sites (MNLD1 and MNLD2) and of the islands investigated for the use or non-use by *M. foina*. Islands 2, 3, 4 in the inset were not object of this study. Small islands are in blue; medium islands are in black; large islands are in red.

6.2.2 Distribution data

The use or non-use by carnivores of the 18 selected sites was investigated with two techniques: scent stations and track surveys. Scent stations were used to attract carnivores to record their tracks and to photograph them with camera traps. Scent stations are often made of a lure or bait and a tracking medium such as sand, track plates or other material (Ray and Zielinski 2008, page 75). In this study, circular scent stations were prepared by mixing the local soil with a mixture of sand and clay (in proportion 1:2) that were easily available along the river channels. They had a diameter of one meter and were created around a small tree which marked the centre of the circle and acted as support for the bait that consisted of butcher discards. This kind of bait was chosen because during the pilot study (see Chapter 2 sections 2.3 and 2.4.2), it resulted to be as successful as other lures or baits that were tried, despite being the least expensive. All the scent stations prepared were baited with the same amount of butcher discards (ca. 50g) and the status of the bait was monitored on a daily basis while checking the scent stations. The bait was seldom consumed by carnivores and it was replaced when necessary. Even when not consumed, bait was replaced every 4-5 days.

Scent stations were positioned 200 meters apart, and their number was proportional to islands or mainland site size. On small islands (Area <1.00 ha), just one scent station was set, while on larger islands (Area ≥1.00 ha) two or three scent stations were set. The number of activated scent stations was 20 on MNLD1 and eight on MNLD2. Scent stations were activated from a minimum of six to a maximum of ten days in each season. They were active for a total of 1646 scent stations nights (924 on the mainland sites and 722 on islands).

The same ten kilometers transect was walked every day, in order to check the scent stations of the mainland sites and of the 16 islands and to record data on mammal tracks and droppings found along the transect (track surveys). The transect path passed through footpaths inside the islands or the mainland sites, and in the matrix surrounding the islands. If a sign was found in a one-five meter strip of soil surrounding the perimeter of a given island, it was assigned to that island. If a supposed *M. foina* and *V. vulpes* track or dropping was found on a scent station or along the ten kilometres transect, a camera trap (Scoutguard SG550, Boly Media Communications Co. Ltd., Kowloon, Hong Kong) was placed in the area to confirm species identification.

6.2.3 Detecting the presence of carnivores

The use of attractants has been demonstrated to be useful in detecting the presence of carnivores and not to generally bias results, provided that the detection distance is small relatively to the animal's home range radius (Gerber et al. 2012). In a study aimed at comparing values of abundance and density of the Malagasy civet (*Fossa fossana*) estimated through data obtained from camera traps with and without lure, Gerber et al. (2012) found that the estimates obtained were comparable. They discuss that, if the maximum distance a carnivore could detect the lure was small compared to its home-range, only animals whose home range already overlapped sampling stations would be attracted.

A study in Italy by Mortelliti and Boitani (2007) has evaluated the probability of presence of *M. foina* in woodland patches of a fragmented landscape by detecting the species' occurrence at lured scent stations. When the authors compared the values of probability of presence in a given patch obtained through scent stations with those obtained through other methods (i.e. track surveys, camera trap surveys and interviews with people), they found comparable values, therefore suggesting that the scent stations method gives unbiased results for studying the use or non-use of a woodland patch by the species.

There is no indication in literature about the detection distance of a lure or bait for martens or small carnivores, but unpublished observations of individuals of *M. foina in the presence of bait*, suggest that a distance of up to 30m is likely (Lapini 2016, personal communication). In the study area this distance is lower than (1) the average value of the minimum distance between two islands in the study area (46.2m±6.4), (2) the average distance between the mainland and the islands (139.5m±94.5) and (3) distance between scent stations used in this study (200m). Therefore the use of a given baited site by *M. foina* should not have influenced the probability of use of the nearest site, given that the species is unlikely to have been able to smell the nearest bait.

In order to have an index allowing to compare values of relative abundance for *M. foina* and *V. vulpes* between the mainland and the islands and between the different seasons, *mainland and islands visiting rates* of the two species were calculated as:

$$seasonal\ visiting\ rate\ = \frac{number\ SS\ visited\ \ in\ xi\ on\ Hi}{total\ number\ SS\ active\ in\ xi\ on\ Hi}\ x\ 100$$

Where:

xi= season (spring, summer, autumn, winter)

Hi= mainland (pull of the data for two sites) or islands (pull of the data for 16 sites).

SS= scent stations

6.2.4 Study design

Carnivore sampling took place between May 2010 and January 2011 for a total of four sampling seasons: spring (May 2010), summer (September 2010), autumn (November 2010) and winter (January 2011). Over the whole study period, besides *M. foina* another species visited scent stations very often, the red fox *(V. vulpes)*. However, the study of habitat use was focused only on *M. foina*, as *V. vulpes* was nearly ubiquitous therefore not allowing for the study of its habitat use. Data showed that islands were seldom visited by *M. foina* and the peak of visiting rate of this species was in autumn (November 2010). This indicated a seasonal variation in the use of islands (Table 6.1), as already observed in other studies on carnivores and river islands (Zoellick et al. 2005).

This seasonal variation in the visiting rate reflects the annual changes which happen in populations of *M. foina* inhabiting Mediterranean habitats*:* in summer and winter adults are visiting their home range in search for food; in spring the patterns of movements for males are strongly dictated by the search for females; in late summer/autumn juveniles usually start to disperse through an “exploring phase” characterised by an increase in home range size (Genovesi et al. 1997). On this basis, it was assumed that the peak in the visiting rate of *M. foina* obtained in autumn on islands was the result of juveniles’ movements through the floodplain in their dispersion phase. This assumption was confirmed by the pilot study of Pavanello (2010) that succeeded in capturing *M. foina* individuals in the study area just in autumn, when five different individuals were captured: they were four juveniles (of which two on the islands and two the mainland) and one adult (on the islands) (see Chapter 2, section 2.3 for further details).

Sandell (1989) observed that, in small carnivores, food can be a factor affecting dispersion, both in females and in males. Therefore, in order to study the influence of food resources on carnivore use of the mainland and island sites of the riverine mosaic of the Tagliamento by *M. foina*, it was decided to focus the data analysis just on autumn data (data obtained in November 2010). By using just data of autumn, the probability that other factors than food and spatial constraints of the landscape would affect use or non-use of a site by *M. foina* inevitably decreased.

6.2.5 Explanatory variables

In this study, using data obtained through scent stations and track surveys, binary response data (presence/absence of *M. foina* on a given patch) were modelled as a function of different explanatory variables through logistic regression using the free software R (R Development Core Team 2012).

Two types of explanatory variables were measured: (1) variables describing the spatial attributes of islands/mainland sites; (2) variables describing abundance of food resources.

Spatial variables

Spatial variables were measured at patch and patch-neighbourhood scale using ArcGIS 9.3, through the Patch Analyst extension for Arcview. 'Patch Neighbourhood' spatial variables of islands and mainland sites were measured within the threshold distance of 1000 meters (edge to edge distance), a scale compatible with the average daily travelling distances of martens (Moriarty 2014; Rondinini and Boitani 2002). The following spatial attributes were measured in each of the 18 patches:

- *area*: size of the mainland or island site (measured in hectares)

- *PI1000:* proximity index within 1000 m from each site (Gustafson and Parker 1994). This index quantifies the spatial context of a habitat patch in relation to its neighbours and to its size and distinguishes sparse distributions of small habitat patches from clusters of large patches;

- *distance to the mainland:* minimum distance from the nearest edge of each island to the mainland (in meters). For mainland sites this distance was set to zero meters.

Food abundance variables

The identification of important food resources in the diet of *M. foina* was based on the available literature. The diet of this species was extensively studied in Italy and what has in general emerged is that the bulk of it is made of fruit and mammals (Genovesi et al. 1996, Balestrieri et al. 2013). *M. foina* is, among small carnivores, the most frugivorous (Genovesi 2003) and fruit is the most abundant item found in its scats (Genovesi et al. 1996). Small mammals also represent an important component in the diet of this Mustelid (Balestrieri et al. 2013; Martinoli and Preatoni 1995). The following variables describing food abundance were measured at each of the 18 sites:

Small mammal annual abundance - Rodents were live-trapped using Sherman trap transects (Sherman Traps, Tallasee, Florida). Traps were spaced 20m from each other along transects. On islands, the number of traps was proportional to island size (min=2 traps, max=39 traps). On the mainland six transects of ten traps each were set to estimate the relative abundance of rodents. Trapping was carried out once per season (summer, autumn, winter and spring) for a total of 1264 trap nights. Traps were baited with a mix of oat and sunflower seeds. Further details on the rodent sampling protocol are provided in Chapter 2, section 2.4). An index of *Apodemus* spp. annual abundance was calculated as the number of unique individuals caught/total number of trap nights per each mainland site and island site.

Fruit annual abundance - Values of cover of shrubs bearing fruits (i.e. *Cornus sanguinea*, *Crategus sp*, *Juniperus communis*, *Ligustrum vulgaris*, *Rosa sp.*, *Rubus sp.*, *Sorbus sp.* and *Prunus sp.*) were measured according to Braun-Blanquet classes, which range between one (sparsely or very sparsely cover present) and five (vegetation covering more than 75% of the area), using random positioned 10x10m quadrats on the islands and on mainland sites. The cover of these shrubs was estimated as the vertical projection of their foliage on the quadrat. Proportional to island size, between one and ten quadrats were sampled in each of the studied islands and a total of 19 quadrats were set on the mainland sites, 14 in site MNLD1 and five in site MNLD2. On islands were number of quadrats was more than one, the minimum distance between two quadrats was 100m. Data were collected in late summer 2010. The values of cover of the selected shrubs were summed up to obtain an indirect index for fruit abundance of each investigated site.

6.2.6 Statistical analysis

Kruskal-Wallis test was applied to evaluate if there was a difference in the presence/absence of the species on each site throughout the four seasons in which the fieldwork was carried out.

Explanatory variables were checked for their statistical distribution using Shapiro-Wilk test and for homogeneity in their variances using Bartlett test. This was done in order to decide which correlation coefficient to calculate and to explore collinearity problems among explanatory variables. Given that some variables did not show a normal distribution, Spearman correlation coefficients were used. Usually correlation coefficients between explanatory variables ≥ 0.70 are used as appropriate indicators for when collinearity could begin to severely distort logistic model estimation (Dormann et al. 2013). Therefore, the threshold of 0.70 was used to distinguish strong correlations from weaker ones.

A residual regression approach was used to handle possible collinearity problems among spatial explanatory variables showing strong Spearman correlations (ρ >0.70) (Graham 2003). Residual regression aims to create new purged explanatory variables by reciprocally subtracting the common variation from the less important variables. It linearly regresses explanatory variables against each other and uses the residuals to represent them (Dormann et al. 2013).

In order to investigate which variables affected *M. foina* use of a given site in autumn, data of its presence/absence in these two seasons were pulled. Logistic regression assumes linearity of explanatory variables and log odds. The existence of any nonlinear relationships was assessed using a series of Generalized Additive Models (GAM). GAMs are a class semi-parametric modelling methods that are able to smooth the data and allow one to detect any nonlinearities (Wood 2006). Four GAMs were fitted the presence and absence data, using one predictor at the time. The presence of nonlinearity was then checked by plotting the smooth functions, obtained from the model fitting procedure. The visual inspection of the fitted models confirmed that all relationships were linear, so no further action was taken when fitting the logistic regression model (i.e. no polynomial terms were included, to take into account nonlinearities). All the GAM analyses were conducted using the mgcv package for R.

Model building and selection

A *full model* was built containing all the explanatory variables that did not show inter-collinearity problems or a non-linear relationship with the log-odds. As the aim of this study was to identify the most important variables explaining the use or non-use of *M. foina* on the 18 investigated sites and therefore the *best model* explaining presence/absence in a site, an informative-theorethic approach was followed for model selection. The MuMIn package of the software R (Barton 2016) was used to identify the best model.

Models were first ranked according to AIC_c (second order Akaike Information Criteria for small sample sizes). AICc is AIC with a greater penalty for extra parameters and it is recommended for small datasets::

$$AICc = AIC + \frac{2k(k+1)}{n-k-1}$$

where n denotes the sample size and k is the number of parameters in the model. Burnham and Anderson (2002) strongly recommend using AICc, rather than AIC, if n is small or k is large. The best model was considered the one with the lowest AICc. To study the significance of the coefficients of the best model, the likelihood ratio test was used. ΔAICc and Akaike weights (wi) were also calculated. Akaike weights can be interpreted as probabilities - the probability that the given model is the best model. The point of the Akaike weights is to place the ΔAICc on a more interpretable scale. Those models with $\Delta AIC_c < 2$ (and $w_i \geq 0.10$) from the top model, were considered as competing, not distinguishable models. Models with $2 \leq \Delta AIC_c \leq 7$ where given less empirical support (candidate models) and models with $\Delta AIC_c > 7$ were given no empirical support (Burnham and Anderson 2002).

Models affected by over-fitting were not considered in the model selection process. Through Moran I test, it was evaluated whether the first ranked models were affected by spatial autocorrelation. Nagelkerke R^2 was calculated as a goodness of fit measure.

6.3 Results

6.3.1 Distribution data

Two species of carnivores were detected through scent stations besides *M. foina* and *V. vulpes*, the badger *(Meles meles)* and the cat *(Felis sp.). M. meles* and *Felis sp.* were recorded in less than 10% of the sampled sites. *V. vulpes* visited scent stations very often and the species was detected in 72% of the sampled sites. In autumn and autumn, *M. foina* was found in 50% of the sampled sites, of which two were the mainland sites MNLD1 and MNLD2, four were large islands (I6, I9, I12 and I18) and three were medium islands (I1, I13 and I17).

Presence absence data of *M. foina* at the 18 investigated sites differed across the four seasons (Kruskal-Wallis χ^2= 6.92, df = 3, p-value = 0.08), as is it also suggested by the variation of the index of mainland/island visiting rate calculated in all the seasons the scent stations were active (Table 6.1). *M. foina* visited the scent stations of the mainland more often than those of the islands in each of the investigated seasons. Islands were seldom visited by *M. foina* and the peak of visiting rate of this species was in autumn.

Table 6.1 Index of *seasonal mainland and islands visiting rate* for the two most common carnivore species detected in the study area (*M. foina* and *V. vulpes*).

	spring	**summer**	**autumn**	**winter**
Martes foina				
Mainland	13.50	5.35	16.55	5.45
Islands	0.56	1.36	7.80	0.00
Vulpes vulpes				
Mainland	6.50	5.76	1.38	1.36
Islands	3.89	4.98	2.84	2.22

6.3.2 Explanatory variables

Seven explanatory variables were taken into consideration for describing the spatial characteristics and the abundance of food resources in each of the investigate sites. Out of these seven variables, two were created by means of residual regression. Their ranges and mean values shown in Table 6.2.

Table 6.2 List of the explanatory variables used in the logistic regression models. Variables are attributes measured in a sample of 18 sites (two on the mainland and 16 on the islands) Area_res and PI1000_res were created through residual regression. TN: trap nights; BB classes=Braun-Blanquet classes.

Variable type	*List of variables*	*range*	*mean ± SD*
Spatial variables	*Area (ha)*	0.1 -4.2	1.0 ± 1.0
	PI1000 - proximity index 1000m	38 - 39	38.49 ± 0.49
	Distance - minimum distance to the mainland (m)	0.0 – 310	127 ±103
	Area_res	-1.1 - 1.0	0.00 ± 0.56
	PI1000_res	-0.6 - 0.5	0.02 ± 0.29
Resource abundance variables	*Small mammal annual abundance* (number of Apodemus spp. individuals / number of TN)	0 - 83	29± 2
	Fruit annual abundance (sum of cover of shrubs bearing fruits estimated in BB classes)	0.1 - 6.2	3.4 ± 1.9

Spatial variables

Strong correlations were found among the variables area, distance and PI1000 (Table 6.3). Following the protocol of Dormann et al. (2013), these three spatial variables were ranked according to their importance in describing the presence/absence of *M. foina* in the study area. In order to rank them, the three variables were singularly regressed against presence/absence of *M. foina* and the regressions were ranked according to their AICc. *Distance* was identified as the most important among those three strongly correlated variables.

Residuals of *area* regressed on distance were used to obtain a new variable (*area_res*) accounting for habitat amount but not correlated with the variable distance. The values of *area_res* increased with increasing patch area and decreasing patch distance to the mainland. Small/medium and distant to the mainland islands had the most negative values of *area_res* (*area_res*≤-0.3: I11, I14, I15, I16). Mainland sites MNLD1- MNLD2 and the largest islands I5-I6-I9 showed the highest values of *area_res* (*area_res* ≥0.5). All the other islands showed intermediate values (-0.2<*area_res*<0.5) and varied between large islands distant to the mainland (i.e. I10, *area_res*=0.4) or large/ medium islands relatively closed to the mainland (i.e I12, I13, *area_res*=0.2).

PI1000 was also regressed on *distance* to obtain a new variable describing site isolation (*PI1000_res*), which was not correlated with the variable distance (see Mortelliti and Boitani 2008 for another application) and *area_res*. Values of *PI1000_res* increased with increasing isolation of island sites in terms of distance from the mainland and of richness of surroundings. Sites with *PI1000_res* <0.0 were prevalently medium islands very close to the mainland or characterized by rich surroundings, i.e. islands that were surrounded by several other islands (I1, I11, I12, I17, I18, I19). Island sites more isolated in terms of distance from the mainland and poorness of surroundings showed values of *P1000_res* ≥ 0.0 (I16, I9, I8, I13, I14, I6, I5, I15, I10, I7). Not considering the mainland, the highest values of *PI1000_res* (i.e. *PI1000_res*≥0.2) was obtained for small island I15, medium island I17 and large island I10. These three islands were the most distant from the mainland. As for the mainland sites, the values of *PI1000_res* showed the highest values

(*PI1000_res*>0.3) because the calculation of PI1000 takes area of a site into account (Figure 6.2A). Through the substitution of the variables *area* and *PI1000* with respectively *area_res* and *PI1000_res*, the strongest correlations among spatial variables were eliminated (Table 6.3).

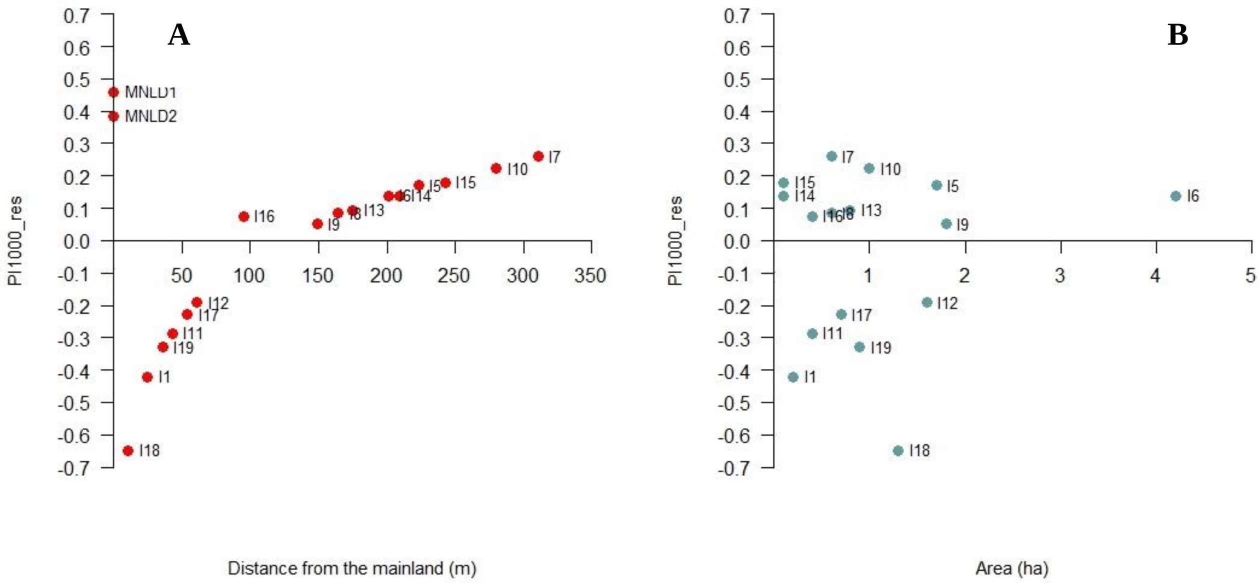


Figure 6.2 Scatterplots showing the relationships between: (A) the variable *PI1000_res* and the variable *distance from the mainland* and (B) the variable *PI1000_res* and the variable *area*. PI1000_res values are the residuals obtained by regressing the variable PI1000 on the variable distance. In (B) values of the mainland are excluded.

Table 6.3 Results for Spearman correlation coefficients (ρ) among all the variables considered for the logistic regression models. Values with one asterisk indicate significant correlations at p≤0.05 level. Values in bold with two asterisks represent very strong correlations (ρ >0.70, p≤0.01). Underlined values of ρ represent strong correlations which have tackled though residual regression. Fruit= fruit annual abundance; small mammals=small mammal annual abundance.

	Area	*Distance*	*PI1000*	*Area_ res*	*PI1000_ res*	*Fruit*
Distance	-0.70*					
PI1000	<u>**0.82****</u>	<u>**-0.85****</u>				
Area_res	0.71*	0.00	0.31			
PI1000_res	0.41*	0.01	0.51*	0.40		
Fruit	0.50*	-0.38	0.43	0.34	0.19	
Small mammals	0.44	-0.44	0.64*	0.12	0.14	0.37

Food abundance variables

The value *of small mammal abundance* increased with increasing site area, showing the lowest values in some of the smallest islands (i.e. II5 and I16 small mammal annual abundance=0.00 individuals/100 trap nights) and the highest on the mainland sites MNLD1 and MNLD2 (values of small mammal abundance respectively equal to 82.8 and 77.8 individuals/100 trap nights).

Fruit bearing shrubs were found at all sites with variable abundances. I19 and I11 showed the lowest fruit abundance (values of summed up Braun Blanquet cover <1, Figure 6.3). Mainland sites MNLD1 and MNLD2, as well as islands I1 (one of the smallest sites) and I12 (large site) showed the highest values of *fruit annual abundance* (fruit annual abundance>5.00). By dividing the investigated sites according to their area into three classes, small sites (area<0.7 ha), medium sites (0.7<area<1.2ha) and large sites (area≥1.2 ha) there was a trend for an increase of fruit annual abundance with the increase of island size (Figure 6.3). A Kruskal-Wallis test also confirmed a difference in the value of fruit annual abundance between the three area classes (Kruskal-Wallis chi-squared = 7.21, df = 2, p-value = 0.02). By removing the value of I1 and of I12 the results of the Kruskal-Wallis test remained significant.

Variables describing food abundance did not show significant correlations with the spatial variables *area_res* and *PI1000_res* (Table 6.2).

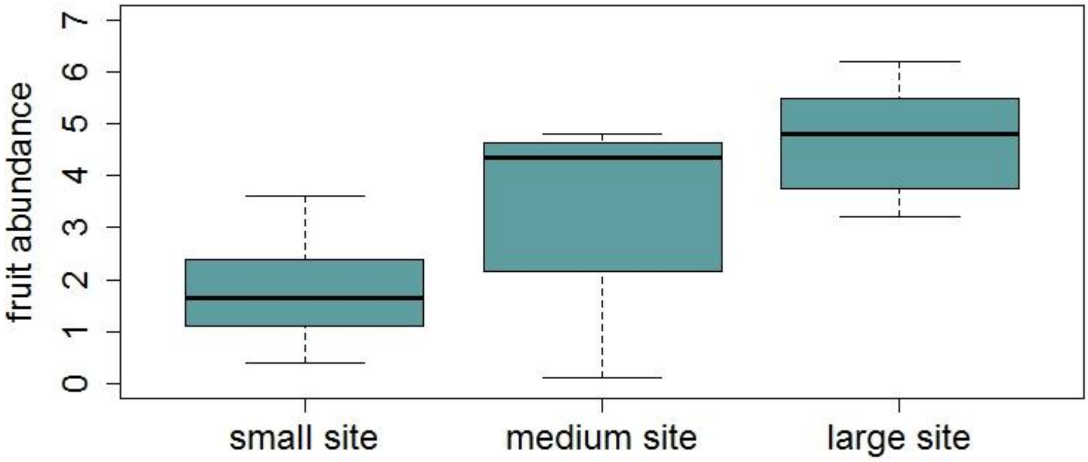


Figure 6.3 Boxplots representing the increasing of the value of fruit cover with the area of the sites under investigation. Small sites: area<0.7 ha; medium sites: 0.7<area<1.2ha; large sites: area≥1.2 ha. Site I1 was not included in the data. Data for the mainland sites are included in the boxplots for large sites. The median, the first and third quartile and 95% confidence interval of median are represented in each of the boxplots.

6.3.3 Model selection

Four variables were selected to build the full model on the basis of the results of the residual regression analysis and of the obtained values of Spearman correlations: area_res, PI1000_res, small mammal annual abundance and fruit annual abundance. These variables did not show collinearity problems and resulted in univariate linear relationships with the log-odds. For the model selection process, a total of 16 models were created with all the combination of the four explanatory variables identified (Table 6.4). Two of them had very high values of the coefficient for *PI1000_res*, being affected by over-fitting (models 14 and model 16 - full model, in Table 6.4), probably due to the small dataset (N=18). Among the remaining 14 models, the one with the lowest AICc was considered the best model, namely model 13 (Table 6.4).

The best model found that probability of presence was almost significantly related to *PI1000_res* (β =-6.92; SE=5.22, p=0.06) and significantly related to *fruit annual abundance* (β=2.75; SE=1.57, p<0.01; Table 6.4). This model had a high goodness of fit (R^2 = 0.84) and was not affected by spatial autocorrelation (Moran I test: I_{obs}= -0.07, I_{exp} = -0.06, SD= 0.09 p=0.93), therefore meaning that the investigated sites are spatially independent and the presence of the animals is not conditioned by the relative spatial distribution of sites. Probability of presence of *M. foina* increased with relative fruit abundance and showed a trend to decrease from the mainland sites, to medium and large islands very close to the mainland (e.g.I1, I11, I12, I18) and was equal to zero in those islands which were distant from the mainland and which were not surrounded by several other islands (e.g. I14, I15, I16). The models with the variable small mammal abundance included were either affected by over-fitting (i.e. model 16) or showed values of ΔAIC_c > 7 (models 6, 8, 12, 2, 10, 4), therefore they were not sustained by empirical evidence. The variable small mammal annual abundance therefore appeared not to be affecting the use or non-use by juveniles of *M. foina* of the investigated mainland an island sites.

Table 6.4 Model selection table presenting the values of the coefficients for each of the 16 models. Models are ranked according to AICc. Models marked with asterisks are those affected by overfitting and therefore not considered in the model selection process. The best model is reported in bold ID=13. SM =small mammal annual abundance, Fruit =fruit annual abundance.

Model ID	***SM***	***Area_res***	***Fruit***	***PI1000_res***	***df***	***AICc***	*ΔAICc*	*weight*
14*	31.68		150.1	-1065.0	4	11.1	0.00	0.65
13			**2.8**	**-6.9**	**3**	**14.7**	**1.85**	**0.10**
16*	3.21	175.30	35.2	-522.8	5	15.0	3.92	0.09
5			1.9		2	15.5	4.46	0.07
15		3.77	3.2	-12.3	4	17.4	6.37	0.03
7		-1.87	2.5		3	17.6	6.52	0.02
6	0.00		1.9		3	18.4	7.37	0.02
8	0.02	-2.06	2.4		4	20.9	9.78	0.00
12	0.14	5.97		-11.7	4	24.5	13.43	0.00
2	0.05				2	26.2	15.09	0.00
10	0.07			-3.4	3	26.8	15.77	0.00
1					1	27.2	16.13	0.00
4	0.05	0.84			3	28.4	17.32	0.00
3		0.77			2	29.0	17.92	0.00
9				-1.1	2	29.3	18.23	0.00
11		1.78		-3.2	3	29.8	18.74	0.00

6.4 Discussion

Four species of carnivores were detected on the mainland and islands of the Tagliamento floodplain: *M. foina*, *V. vulpes*, *M. meles* and F. *sylvestris*. Two species were very rare, namely *M. meles* and *F. sylvestris* , while two species were present relatively often, namely *M. foina* and *V. vulpes*. Both these species were more present on the mainland than on the islands in all seasons (Table 6.1). However, the frequency of presence of *M. foina* on the islands increased remarkably in the autumn, when juveniles are likely to disperse.

6.4.1 The use of scent stations as a way of detecting carnivores

Every carnivore needs to weight the reward of bait against the risks of travelling to it. Martens are reluctant to venture into openings (Cushman et al. 2011) because they are risk-adverse (Zelinski and Long personal communications) and hence have to trade-off the benefit of a food reward represented by a bait against the risk of predation. The willingness to travel the distance to the bait source on the scent stations through the gravel matrix, would be therefore obviously a relevant issue for *M. foina* individuals moving across the Tagliamento mosaic even if they were to be close enough to smell the bait. A recent study by Moriarty et al. (2015) showed that detection of the American martens (*M. caurina*) at baited stations may not represent habitat use in the winter, when there is a decrease in the abundance of potential preys like small mammals: the authors found that in periods of increased motivation due to hunger or intense curiosity, martens were detected also in non-preferred habitat types characterised by low vegetation cover and therefore increased predation risk. This could not have happened on the Tagliamento, given that over the autumn, both the mainland and island sites offer a high abundance and selection of berries and fleshy fruits to be eaten by *M. foina*. The riparian forest in the tract under investigation, holds a higher diversity of fruit bearing shrubs and trees (e.g., *Rosa* sp, *Prunus* sp, *Sorbus* sp., *Juniperus* sp.) than the abutting surrounded cultivated land, while on the river islands shrubs of *Crategus* sp, *Rubus* sp and *C. sanguinea* are the most abundant species (Edwards et al. 1999; Kollmann et al. 1999).

It was therefore concluded that given (1) that all the investigated sites had the same probability of attracting individuals of *M. foina*, because all of them were baited with the same amount of bait which was constantly present on scent stations; (2) that in autumn the availability of food resources represented by fruit and small mammals is high at the study site; (3) that martens are reluctant to adventure in open habitats; and (4) that the attraction distance for baits for *M. foina* is likely to be in the range of 30m, the presence of the bait on scent stations in this study should not have biased the results obtained.

6.4.2 Factors affecting M. foina use of the Tagliamento floodplain

If we accept that the presence of the bait did not influence habitat use by *M. foina*, then following the predictions stated in the introduction, this study showed that the abundance of food resources in the mainland and island sites of the Tagliamento riverine mosaic significantly affected the probability of use of a given habitat by *M. foina* in autumn. Between the two kinds of food resources taken into consideration in the study, just abundance of fruit turned out to be significant in determining the use or non-use of a given landscape element by this species. *M. foina* used sites characterised by high abundance of fruit. This is in line with previous observations found in Mediterranean areas, where carnivores have a much higher rate of fruit consumption than elsewhere (Rosalino and Santos-Reis 2009). Given that riparian corridors, especially when naturally conserved, can offer a wide variety of fruit bearing trees and shrubs, they have shown to represent very important habitats for carnivores conservation (Matos et al. 2009). Fruit is a seasonal item, but dietary studies on *M. foina* showed that it is consumed also during the cold months, even if a shift to *Apodemus spp*. in autumn and to birds in winter are quite common (Serafini and Lovari 1993).

Furthermore a trend emerged which showed that individuals did not use the smallest and most isolated sites, probably because they were characterised by both low fruit abundance and a high degree of isolation in the floodplain (i.e. islands I14, I15 and I16). For most carnivore species, requirements for food and shelter have been shown to shape movements in the landscape: use of suitable habitat patches is not often related to their proportional availability, but rather some patches are used more than others because they are easy to reach, while others are avoided because they are too isolated or offer no energetic advantage (Cervinka et al. 2011; Guthlin et al. 2013; Mortelliti and Boitani 2008).

As previously outlined, this non-use of isolated patches might be due to a predator-avoidance behaviour of *M. foina*, by which this species bypasses places with low vegetation cover. Riparian vegetation acts as cover to avoid encounters with predators. Besides local hunters with their dogs, bird of prey species like the Eurasian eagle-owl (*Bubo bubo*) and the black kite (*Milvus migrans*) are in fact common in the study area (Parodi 2004). Among other martens, the need for cover is particularly well documented in American martens (*M. americana*): they prefer vegetation with a complex structure and seldom venture into open areas (Buskirk and Powell 1994; Moriarty et al. 2015). It is quite plausible that *M. foina* avoided reaching the smallest and most isolated islands (I14, I15 PI_1000res $\geq$ 0.5) because it would have been dangerous for the species to cross the open gravels. A visit to these islands from the mainland would involve a c. 250 meters walk across these gravels with little possibility of finding emergency cover. The risk of being predated would not be compensated by the amount of resources offered by these small islands, where fruit annual abundance was found to be low and where individuals of *Apodemus spp.* were not trapped at all.

6.4.3 Conclusions

Carnivores occupying large home ranges are umbrella species (Roberge and Angelstam 2003) and are particularly susceptible to the structure and dynamics of their habitats (Schonewald-Cox et al. 1998). It is therefore useful to understand the critical variables driving the use of habitats in natural riparian mosaics by carnivores in order to effectively engage in river conservation and management programs along degraded rivers around the world. This study confirms that abundance of food resource and their spatial constraints within the landscape affect the use of a given habitat patch by carnivores also in riparian mosaics. For river restoration projects, it would be important to preserve islands, especially clusters of islands, in order to ensure connection and facilitate animal movements across the riparian corridor.

Finally in the context of this thesis results suggest that the predator pressure of carnivores on small mammals on riverine islands is lower than that on the mainland, suggesting that the mainland-island system of the River Tagliamento fits just partly into the theories of island biogeography. This point will be widely discussed in the following chapter.

6.5 References

Balestrieri, A., Remonti, L., Capra, R.B., Canova, L., Prigioni, C., 2013. Food habits of the stone marten (Martes foina) (Mammalia: Carnivora) in plain areas of Northern Italy prior to pine marten (M. martes) spreading. Italian Journal of Zoology 80, 60-68.

Barton, K., 2016. MuMIn: Multi-model inference. R package version 1.15.6.

Burnham, K. P., Anderson, D. R., 2002. Model Selection and Multimodel Inference. A Practical Information-Theoretic Approach. Springer-Verlag New York.

Buskirk, S.W. and Powell, R.A., 1994. Habitat ecology of fisher and American marten, In The biology and conservation of martens, sables and fishers. ed. S.W. Buskirk, pp. 283-296. Cornell Univesity Press, Ithaca.

Cervinka, J., Salek, M., Pavluvcik, P., Kreisinger, J., 2011. The fine-scale utilization of forest edges by mammalian mesopredators related to patch size and conservation issues in Central European farmland. Biodiversity and Conservation 20, 3459-3475.

Clerici, N. and Vogt, P., 2013. Ranking European regions as providers of structural riparian corridors for conservation and management purposes. International Journal of Applied Earth Observation 21, 477-583.

Crabtree, R.L. and Wolfe, M.L., 1988. Effects of alternate prey on skunk predation of waterfowl nests. Wildlife Society Bulletin 16, 163-169.

Crooks, K.R. and Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400, 563-566.

Crooks, K.R., 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16, 488-502.

Cushman, S.A., Raphael, M.G., Ruggiero, L.F., Shirk, A.S., Wasserman,T.N., O'Doherty, E.C., 2011. Limiting factors and landscape connectivity: the American marten in the Rocky Mountains. Landscape Ecology 26, 1137–1149

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27-46

Duebbert, H.F., Lokemoen, J.T., Sharp, D.E., 1983. Concentrated nesting of mallards and gadwalls on Miller Lake Island, North Dakota. Journal of Wildlife Management 47, 729-740.

Edwards, P.J., Kollmann, J., Gurnell, A.M., Petts, G.E., Tockner, K., Ward, J.V., 1999. A conceptual model of vegetation dynamics on gravel bars of a large Alpine river. Wetlands Ecology and Management 7, 141-153.

Genovesi, P., Secchi, M., Boitani, L., 1996. Diet of the stone marten: an example of ecological flexibility. Journal of Zoology, London 238, 545-555.

Genovesi, P., Sinibaidi, I., Boitani, L., 1997. Spacing patterns and territoriality of the stone marten. Canadian Journal of Zoology 75, 1966-1971.

Genovesi, P., 2003. Faina (Martes foina), In Fauna d'Italia Mammalia: Carnivora Artiodactyla. eds L. Boitani, S. Lovari, A. Vigna Taglianti (eds), pp. pp 113-223. Calderini, Bologna.

Gentili, S., Sigura, M., Bonesi, L., 2014. Decreased small mammal species diversity and increased population abundance along a gradient of agricultural intensification. Hystrix 25, 39-44.

Gerber, B.D., Karpanty, S.M., Kelly, M.J., 2012. Evaluating the potential biases in carnivore capture-recapture studies associated with the use of lure and varying density estimation techniques using photographic-sampling data of the Malagasy civet. Population Ecology 54, 43-54.

Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84, 2809-2815.

Gustafson, E.J. and Parker, G.R., 1994. Using an index of habitat patch proximity for landscape design. Landscape and Urban Planning 29, 117-130.

Guthlin, D., Storch, I., Kuchenhoff, H., 2013. Landscape variables associated with relative abundance of generalist mesopredators. Landscape Ecology 28, 1687-1696.

Haapakoski, M., Sundell, J., Ylönen, H., 2013. Mammalian predator-prey interaction in a fragmented landscape: Weasels and voles. Oecologia 173, 1227-1235.

Hammond, M.C. and Mann, G.E., 1956. Waterfowl nesting islands. Journal of Wildlife Management 20, 345-352.

Indermaur, L., Gehring, M., Wehrle, W., Tockner, K., Naef-daenzer, B., 2009. Behavior-based scale definitions for determining individual space-use: requirements of two amphibians. The American Naturalist 173, 60-70.

Luck, G.W. and Daily, G.C., 2003. Tropical countryside bird assemblages: Richness, composition, and foraging differ by landscape context. Ecological Applications 13, 235-247.

Kollmann, J., Vieli, M., Edwards, P.J., Tockner, K., Ward, J.V., 1999. Interaction between vegetation developement and island formation in the Alpine river Tagliamento,Applied Vegetation Science 2, 25-36.

Martinoli, A. and Preatoni, D.G., 1995. Food habits of the stone marten (Martes foina) in the upper aveto valley (Northern Apennines, Italy). Hystrix 7, 137-142.

Matos, H., Santos, M., Palomares, F., Santos-Reis, M., 2009. Does riparian habitat condition influence mammalian carnivore abundance in Mediterranean ecosystems? Biodiversity and Conservation 18, 373-386.

Moriarty, M., 2014. Habitat Use and Movement Behaviour of Pacific Marten (*Martes caurina*) in Response to Forest Management Practices in Lassen National Forest, California. PhD Thesis, Oregon State University, US.

Moriarty, K.M., Epps, C.W., Betts, M.G., Hance, D.J., Bailey, J.D., Zielinski, W.J., 2015. Experimental evidence that simplified forest structure interacts with snow cover to influence functional connectivity for Pacific martens. Landscape Ecology 30, 1865-1877.

Mortelliti, A. and Boitani, L., 2007. Evaluation of scent stations survey to monitor the distribution of three European carnivore species (Martes foina, Meles meles, Vulpes vulpes) in a fragmented landscape. Mammalian Biology 73, 287-292.

Mortelliti, A. and Boitani, L., 2008. Interaction of food resources and landscape structure in determining the probability of patch use by carnivores in fragmented landscapes. Landscape Ecology 23, 285-298.

Mortelliti, A., Amori, G., Annesi, F., Boitani, L., 2009. Testing for the relative contribution of patch neighborhood, patch internal structure, and presence of predators and competitor species in determining distribution patterns of rodents in a fragmented landscape. Canadian Journal of Zoology 87, 662-670.

Naiman, R.J., Decamps, H., Pollock, M.M., 1993. The role of riparian corridors in mantaining regional biodiversity. Ecological Applications 3, 209-212

Paquet, P.C., Alexander, S.M., Swan, P.L., Darimont, C., 2006. Influence of natural fragmentation and resource availability on distribution and connectivity of gray wolves (Canis lupus) in the archipelago of coastal British Columbia Canada. In: Crooks, K.R., Sanjan, M., (eds). Connectivity conservation. Cambridge University press, Cambridge, 130-156.

Parodi, R., 2004. Avifauna in provincia di Pordenone. Provincia di Pordenone, Pordenone.

Pavanello, M., 2010. Studio delle comunità di piccoli mammiferi in un ambiente naturale frammentato: le isole del fiume Tagliamento. MSc Thesis, Department of Life Sciences, Trieste University.

Prigioni, C., Balestrieri, A., Remonti, L., Cavada, L., 2008. Differential use of food and habitat by sympatric carnivores in the eastern Italian Alps. Italian Journal of Zoology 75, 173-184.

R Developmental CoreTeam: A language and environment for statistical computing, ed. R.F.f.S. Computing, Vienna, Austria.

Ray, G.C. and Zielinski,W.J., 2008. Track stations. In: Long, R.A., MacKay, P., Ray, J., Zielinski, W (eds). Non-invasive Survey Methods for Carnivores. Island Press, Washington.

Roberge, J.M. and Angelstam, P., 2003. Usefulness of the umbrella species concept as a conservation tool. Conservation Biology 18, 76-85.

Rondinini, C. and Boitani, L., 2002. Habitat use by beech martens in a fragmented landscape. Ecography 25, 257-264.

Rosalino, L.M. and Santos-Reis, M., 2009. Fruit consumption by carnivores in Mediterranean Europe. Mammal Review 39, 67-78.

Rust, C., 1998. Die okologische Bedeutung von Inseln und Schotterbanken im Tagliamento (Friaul, Italien) am Beispiel der Laufkaferzonose (Carabidae, Insecta). Diplomarbeit, ETH Zurich.

Sandell, M., 1989. The mating tactics and spacing patterns of solitary carnivores. In: Gilleman, J.L. (eds.), Carnivore behaviour, ecology, and evolution. Chapman and Hall, London. (pp. 164-182).

Santos, M.J., 2010. Encroachment of upland Mediterranean plant species in riparian ecosystems of southern Portugal. Biodiversity and Conservation 19, 2667-2684.

Santos, M.J., Matos, H.M., Palomares, F., Santos-Reis, M., 2011. Factors affecting mammalian carnivore use of riparian ecosystems in Mediterranean climates. Journal of Mammalogy 92, 1060-1069.

Schonewald-Cox, C., Azari, R., Blume, S., 1998. Scale, variable density and conservation planning for mammalian carnivores. Conservation Biology 5, 491-495.

Sovada, M.A., Sargeant, A.B., Grier, J.W., 1995. Differential effects of coyotes and red foxes on duck nest success. Journal of Wildlife Management 59, 1-9.

Stephens, D.W. and Krebs, J.R., 1986. Foraging Theory. Princeton University Press, Princeton.

Swihart, R.K., Gehring, T.M., Kolozsvary, M.B., Nupp, T.E., 2003. Responses of 'resistant' vertebrates to habitat loss and fragmentation: The importance of niche breadth and range boundaries. Diversity and Distributions 9, 1-18.

Tockner, K., Ward, J.V., Arscott, D.B., Edwards, P.J., Kollmann, J., Gurnell, A.M., Petts, G.E., Maiolini, B., 2003. The Tagliamento river: a model ecosystem of European importance. Aquatic Science 65, 239-253.

Virgos, E. and Garcia, F.J., 2002. Patch occupancy by stone martens (Martes foina) in a fragmented landscapes of Southern Spain: the role of fragment size isolation and habitat structure. Acta Oecologica 23, 231-237.

Wiens, J.A., 1989. Spatial scaling in ecology. Functional Ecology 3, 383-397.

Wood, S., 2006. Generalized Additive Models: an introduction with R. CRC Press.

Zabala, J., Zuberogoitia, I., Garin, I., Aihartza, J., 2003. Landscape features in the habitat selection of European mink (Mustela lutreola) in south-western Europe. Journal of Zoology 260, 415-421.

Zoellick, B.W., Ulmschnelder, H.M., Stanley, A.W., 2005. Distribution and composition of mammalian predators along the snake river in southwestern Idaho. Northwest Science 79, 265-272.

Zollner, P.A. and Lima, S.L., 2005. Behavioral tradeoffs when dispersing across a patchy landscape. Oikos 108, 219-230.

Chapter 7 - General discussion

The thesis has examined the distribution, demographic and spatial differences of three small mammal species in the context of a riparian landscape characterized by the presence of river islands that are relatively isolated from the riparian forest and hence comparable to other kinds of isolated habitats. The expectation was that at least some of the patterns that have been extensively studied and observed on oceanic or continental islands, and that gave rise to accepted paradigms like the Theory of Island Biogeography (MacArthur and Wilson 1967) and the island syndrome, would be found on islands of the River Tagliamento as well. This study has demonstrated that while some of the patterns observed for oceanic or continental islands do occur in the studied landscape, other patterns do not.

Amongst the patterns that did fit the known paradigms were a decreased species diversity going from the mainland to the islands (Theory of Island Biogeography), increased densities and a relatively higher proportion of adults for *A. sylvaticus* only (island syndrome), and significantly greater home ranges on islands for *A. agrarius* (island syndrome). However, other patterns did not fit. *A. flavicollis* and *A. agrarius* did not follow the island syndrome predictions for most of the life-history traits considered. Nor *A. sylvaticus* did follow the island syndrome prediction for reproductive output and body weight. This suggests that the degree of isolation of the islands in our system is not high enough for the patterns to fully resemble those expected for oceanic islands. Moreover, the Tagliamento system is also affected by periodically disruptive events, namely floods that reset the system favouring those species that are more arboreal, and hence have greater chances of survival like *A. sylvaticus,* besides a greater ability to re-colonise.

This discussion focuses on the main findings of the thesis in the context of the main theories of island biogeography and landscape ecology and in relation to the wider literature. The main findings were: 1) A reduced species diversity on river islands; 2) Over-representation of generalist species on islands; 3) Larger home ranges of *A. agrarius* on islands; 4) Reduction of predator species on islands; 5) A difference in some life-history traits on islands. It then considers all the factors that have been examined against those listed by Adler and Levins (1994) and Vicente (1999) as typical of oceanic island communities and against those described for animal communities inhabiting habitat islands, to check to what degree the Tagliamento system fits predictions made for oceanic islands and to what degree it fits evidences found in landscape ecology.

7.1 Reduced species diversity on river islands

A reduced species diversity on islands is one of the main predictions of the theory of Island Biogeography (MacArthur and Wilson 1967). This reduction for oceanic islands is due to the difficulty in reaching islands for vertebrates, and is a function of the distance of the island from the mainland and of island size. The composition of the whole community of mammals on the Tagliamento riparian mosaic was not studied systematically in this thesis, but a significant difference in the composition of the *Apodemus* community spp. between the mainland and the river islands was observed.

Reduced species diversity in relation to distance and size has been observed also for *habitat islands, 'a spatially delimited portion of remnant habitat differing from its surroundings'* (Forman and Godron 1981). Mammal species richness and diversity have been shown to covariate with area and isolation in fragmented landscapes worldwide (Debinski and Holt 2000; Magnus and Cáceres 2012). The general trend is a significant reduction in the species richness and diversity in relation to a decreased size and increased isolation of habitat islands (e.g. Charles and Ang 2010; Goodman and Rakotondravony 2000; Hanser and Huntly 2006; Negro et al. 2009; Nupp and Swihart 2000; Pardini et al. 2010; Stevens and Husband 1998; Vieira et al. 2009), as for oceanic islands. In some cases though, the effects of area and isolation on species richness and diversity of habitat islands are not comparable to those of oceanic islands. In a few studies on mammals, it emerged that mammal species richness and diversity did not increase with habitat island size (e.g. Lomolino and Smith 2003; Silva 2001) or did not decrease with isolation (e.g. Harcourt and Doherty 2005; Lomolino and Perault 2001). Moreover, small mammal species diversity has sometimes displayed correlations with absolute and proportional abundance and/or diversity of shrubs of habitat islands (e.g. Hanser and Huntly 2006; Michel et al. 2006) and even to increase following fragmentation, if species which tolerate or exploit the matrix are numerous in the community, since their abundance following fragmentation can increase (e.g. Gascon et al. 1999).

The results found here indicate that the number of *Apodemus* species found on the mainland and on all islands together was the same (N=3), but *Apodemus* species diversity estimated through the Simpson's index, that takes also species' relative abundance into account, increased with island size, as already found in several other landscape ecology studies carried out on small mammals (e.g. Bolger et al. 1997; De La Sancha 2014; Hanser and Huntly 2006; Pardini et al. 2005) and other taxa (e.g. Bossart et al. 2006; Collinge 1995 for *insects;* Russildi et al. 2016 for *amphibians*). By considering relative abundances, this index was useful for comparing species' interactions on each island of the Tagliamento and to formulate hypotheses explaining the observed patterns on the basis of mechanisms of interspecific competition and niche width.

The effect of habitat island area on *Apodemus* species diversity identified through path analysis (chapter 3), was explained as being a consequence of greater diversity of shrub species carrying seeds on larger islands (which allows the coexistence of all the three species on them) and of bigger resistance to flooding of these islands. During the course of the study two big floods were observed occurring in early November and in late December 2010 and other floods of more moderate entity in May, August and October 2010. In the landscape under study floods had a stronger effect on small and medium islands than on large islands, since the latter show relatively higher elevations on top of the gravel bars (up to 2-3m, due to repeated episodes of sediment deposition) in respect to small islands, therefore being less frequently inundated.

In general, species diversity is a measure of the number of component species and their abundance at a defined point in space and time (Rosenzweig 1995). The effect of floods on small mammal species diversity in natural riparian habitats has never been investigated, but Hanley and Barnard (1999) found that other variables, such as small mammal abundance, could be strongly influenced by floods. Indeed, the effect of floods on small mammal diversity for this study on the Tagliamento was a direct consequence of floods affecting the relative abundance of single species, therefore inducing a difference in the value of species diversity calculated through the Shannon index, i.e. higher values of relative abundance for single species correspond to higher values of Shannon index in larger islands (see chapter 3, section 3.3.1, Table 3.1); a disruptive event like a flood, by reducing or resetting the abundance of small mammals on islands would also directly reduce their diversity with a larger impact on small islands which in the study area show less resilience to such events (Kollman et al. 1999). Indeed, in the study area after the flood of November, the abundance of *A. flavicollis* was reset in nine islands, five of which were small and medium islands. For *A. agrarius*, its abundance was reset in three islands, two of which were medium islands (it was never captured on small islands). Abundance of *A. sylvaticus* was reset in two islands, one small and one medium. Similar results were obtained after the flood of early December. *A. flavicollis* disappeared from two islands (one small, one medium), *A. agrarius*' abundance was reset in one large island while the abundance of *A. sylvaticus* was reset in three islands (two of which were small and medium) (see chapter 4, Appendix 4.1).

These results indicate the big impact floods can have on the species diversity of small and medium islands, but they should be also discussed in view of the climbing capability of the three species, which likely affects their capacity to face a flood. *A. sylvaticus* and *A. flavicollis* are good climbers and beside burrows, they also frequently use ground and above-ground nests (Sarà 2008; Stepankova and Vohralik 2009). *A. agrarius* is more subterranean and fossorial than the other two species, showing a burrowing mode of life (Kuncova and Frynta 2009). Therefore the low densities of *A. agrarius* on islands could have been due, besides the less favourable conditions as habitat for this species described below (see section 7.5.2), also to its higher risk of drowning following island inundation. This would create fewer re-colonization sources and fewer survivors from the surrounding islands to re-found new populations and suggests islands could be re-colonised more easily by the other two species, which showed in general higher population densities (see chapter 3, Table 3.1 and chapter 4, Appendix 4.1) and good climbing skills.

Nevertheless, *Apodemus* species diversity was not affected by isolation as predicted by the MacArthur and Wilson model (MacArthur and Wilson 1967). But unlike true islands, the Tagliamento river islands are more similar to habitat islands in that they are part of a complex landscape mosaic where the presence and abundance of a given species is function not only of patch size and isolation, but also of how a species perceives the intervening matrix and by its ability to disperse through it (Andren 1994; Ricketts 2001; Rosenblatt et al. 1999) and of the disturbance events (see Fox and Fox 2000 for another example).

Matrix permeability is determined by the structural similarity between matrix habitat and remnant habitats (Kupfer et al. 2006). In the Tagliamento riparian mosaic the difference in the structure of the matrix and the islands is quite substantial given that the matrix is composed by bare gravel and the islands are fragments of riparian woodland. This substantial difference would let us hypothesize that small mammals are not so prone to leave islands and move through the matrix. The presence of environmental cues like hedgerows acting as corridors has shown to help small mammals to keep a straight direction when searching for a new habitat (like a habitat patch) in a hostile matrix and moving along these cues has proved to be an efficient strategy compared to random walking, because it minimizes time spent in the matrix (Zollner and Lima 1999). But proper environmental cues connecting islands are not present on the Tagliamento gravel bars, therefore the movements of mice in the matrix are likely to be more dangerous in that it would expose animals to a higher predation risk (Hansbauer et al. 2008; Wolff and Barret 2008).

High dispersal ability may allow species to re-colonize fragments or maintain high immigration rates also in isolated patches surrounded by a permeable matrix (Sozio and Mortelliti 2015). The dispersal ability depends, among other factors, on species' perceptual range (Prevedello and Vieira 2010), which is defined as the maximum distance at which an animal can perceive the surrounding landscape elements (i.e. a habitat patch) (Zollner and Lima 1997). A recent study by Sozio et al. (2013) investigated the perceptual ranges of *A. sylvaticus* and *A. flavicollis* when released in a bare field surrounding a forest patch. They found that in absence of environmental cues (e.g. hedgerows) the two species move randomly in a bare field. Furthermore, *A. flavicollis* when released in the bare filed matrix was shown to be able to perceive the presence of a wood patch at a maximum of 40m, while for *A. sylvaticus* this upper range was 100m. These data are not available for *A. agrarius*. The authors discussed that these different perceptual ranges reflected their dispersal capabilities and habitat specialization.

Of the three investigated species, *A. sylvaticus* is the most generalist one and is characterised by very high dispersal abilities (Marsh and Harris 2000). *A. flavicollis* has also high dispersal ability but it is more dependent on forest habitat than *A. sylvaticus* (Marsh and Harris 2000). *A. agrarius* is a species linked to agricultural fields and one that uses forest environments occasionally. In fragmented landscapes it has been found to be able to move over distances up to 1.5 kilometres (Kozakiewicz et al. 1999).

The lack of a marked effect of habitat island isolation on *Apodemus* species diversity that emerged in this thesis was likely due to the absence in the study area of a total impermeable matrix surrounding islands (at least in conditions of low flow) and to the short distances, compared to the dispersal abilities of the three species, separating the mainland from the islands. The substantial difference in the structure of the matrix and the island habitats of the Tagliamento could be indeed somehow modulated by the presence throughout the gravel alluvial matrix of small pioneer islands and large woody debris (sensu Edwards et al. 1999). These landscape elements have proved to act as temporal nests and refuges from predators or to provide valuable resources for small mammal survival (Steel et al. 1999) and can therefore facilitate movements of *Apodemus* spp. in the otherwise inhospitable matrix.

In summary, river islands of the Tagliamento fit partly into the general patterns which have emerged for variation of species diversity in landscape ecology studies focused on small mammals; i.e. there was a significant effect of area and a lack of an isolation effect in regulating the values of *Apodemus* spp. diversity on the islands of the Tagliamento. As for other types of landscapes, the relationship between area and species diversity was determined by the higher availability of food resources on larger islands in respect to the smaller ones, which likely allowed for the coexistence of the three mice species by providing enough food resources for all of them. The disruptive effect of floods, which periodically reset the value of species diversity on these islands, is somehow softened by the lack of permanent isolation of these islands from the mainland, by the relatively short distance in-between islands (which make re-colonization events fairly easy) and by the presence of a relatively permeable gravel matrix surrounding islands. Moreover, differences in individual species niche width, adaptability and dispersal abilities are likely to be fundamental in determining the patterns of their relative densities on islands, as will be further explained in the next sections.

7.2 Over-representation of generalist species on islands

The composition of the *Apodemus* community on the Tagliamento mosaic reflected different gradients of species densities moving across the floodplain: indeed, moving from the islands to the mainland, a clear trend of increasing density of the specialist species associated with more mature forest or agricultural habitats, respectively *A. flavicollis* and *A. agrarius*, was observed on one hand and, on the other hand, an opposite downward trend of density of the more generalist species, *A. sylvaticus*, which was found to be the most dense and widespread species on islands. This emergent distribution pattern was most probably not random but indicative of underlying roles of specific ecological mechanisms determining density compensation of *A. sylvaticus* on islands.

These mechanisms have been investigated in several empirical studies revealing that in areas where habitat fragmentation occurs, generalist species predominate, in contrast with specialists that prefer large, connected, high quality areas (e.g. Nupp and Swihart 2001; Sozio and Mortelliti 2015; Youngentob et al. 2012). When life history or other intrinsic differences between species do not exist or are insufficient to generate niche differences between species, coexistence can occur if the competitive environment is spatially heterogeneous (Amarasekare 2003). In this case the generalist species exploits fragmented habitats more efficiently than specialists, being a stronger competitor for resources in such conditions. Under this mechanism specialist species would eventually be excluded from more fragmented sites through interference and resource exploitation competition.

Alternatively, when differences in life histories and/or in the way species exploit resources are intrinsic to the species themselves and do not depend on the species' abiotic or biotic environment, the competitive environment is called homogeneous (Amarasekare 2003). In other words species do not exhibit differential responses to the environment. When the competitive environment is spatially homogeneous, coexistence is most likely to occur via inter-specific trade-offs between life history attributes that influence competition (e.g. fecundity, longevity) and those that allow species to escape or minimize competition (e.g. dispersal) (Amarasekare 2003). Under this possible mechanism habitat specialists are intrinsically more prone to extinction in fragmented contexts (e.g. due to the disruption of their dispersal ability or demography). As a consequence, generalists are able to exploit vacant habitats where competitive pressure has been released (e.g. Diaz et al. 1999; Nupp and Swihart 2000). Under this mechanism, generalists would be favoured as a result of their higher colonization ability (Amarasekare 2003).

Findings of this thesis suggest that the distribution pattern observed for *Apodemus spp*. is likely the result of the first mechanism, namely that generalists dominate in the more fragmented contexts and consequently specialists are reduced in numbers through interference and competition. The floodplain of the Tagliamento is a highly fragmented landscape and islands are characterized by lower abundance of tree cover and seed-bearing shrub species with respect to the mainland. Lawlor (1982) discussed that a decline in the abundance of plant species on islands would result in decreased food supplies (i.e. reduced diversity of seeds), which appear to be a more limiting factor to specialists (i.e. *A. flavicollis* and *A. agrarius* in this study) compared to species which have more catholic diet and habitat preferences or which do not feed mainly on particulate resources (*A. sylvaticus*) and indeed this is what was found for the islands of the River Tagliamento, where *A. sylvaticus* was the most abundant species on islands. Dietary generalists such as *A. sylvaticus* are able to exploit a greater variety of food resources, which may include seeds, fruit, invertebrates and leaves (Hansson 1985). In insular settings their generalist habits may actually provide them with a greater diversity and abundance of resources because, in contrast to seed specialists, they can capitalize on the increased availability of different kinds of food created by a reduction in the number of competitors. Moreover, the ability to shift from one diet to another allows generalist species to avoid effects of seasonal changes in availability of a single resource.

Nevertheless it cannot be ruled out that the difference in the perceptual range of *A. flavicollis* and *A. sylvaticus* revealed by Sozio and Mortelliti (2015) and described in the previous section, could also partly explain the nearly ubiquity of *A. sylvaticus* on islands. The fact that *A. sylvaticus* is more efficient in perceiving a nearby woodland patch when released in a bare matrix, directly affects its dispersal capability and therefore might also increase its efficiency to re-colonise and colonise new islands in the Tagliamento floodplain.

The results presented here therefore indicate that the composition of the communities of small mammals species in the riparian floodplain of Tagliamento reflects trends observed in other terrestrial landscapes characterised by continuous and patchy areas, in that generalist species (*A. sylvaticus* in the study area) being more adaptable, thrive in the patchy/fragmented areas where they succeed in increasing their densities and in negatively interfering with specialists (*A. agrarius* and *A. flavicollis* in the study area), which conversely predominate and thrive in the continuous areas of the landscape. Moreover results suggest also that the higher dispersal capability of *A. sylvaticus*, emerged from other studies, might also be responsible of its nearly ubiquity on the investigated riverine islands.

7.3 Larger home ranges of *A. agrarius* on islands

Comparative analyses of the spatial behaviour of insular and mainland populations of mammals have demonstrated some relevant differences. Individuals from island populations generally have reduced home-range sizes likely as a consequence of (1) increased densities of animals on islands (i.e. increased intraspecific or interspecific competition) (2) increased resource availability for the species that succeeds in living on islands (Sale and Arnould 2009).

In this research on the Tagliamento, male individuals of *A. agrarius* on the islands were found to move over larger areas (average home range size=2.9ha±1.4), compared to animals moving on the mainland (average home range size=0.7ha±0.4). This trend was opposite compared to previous evidence found for other rodent species inhabiting oceanic mainland-island system (e.g. Hare 2009). Considering the home range as circular, these areas would imply an average range length of ~90m on the mainland and of ~110m on islands (i.e. diameter of the circular home range). As proved by results reported in chapter 5, this difference was likely to be mainly due to a decrease in the availability of food resources moving from the mainland to the islands and to their patchy distribution. Moreover a general trend for a decreased density of competitors and conspecifics was also found on the islands in respect to the mainland. Statistical analysis revealed also a significant role of distance of the activity range from an edge habitat as a factor affecting animals' home range size when moving across the riparian mosaic.

The relation between food availability and home range size in small mammals has been largely proved both in continuous (Harris and Leintner 2004; Jonsson et al. 2002; Shradin and Pillay 2006) and in fragmented terrestrial habitats. In the latter, the patchy distribution of resources leads animals to move over larger distances to acquire necessary resources for their daily activities (e.g. Relyea et al. 2000). In terrestrial fragmented landscapes, when critical resources are more widely dispersed within and among small patches, mammals utilize larger and more spatially disparate areas to satisfy their metabolic and reproductive needs. As an example, a study on raccoons (*Procyon lotor*) inhabiting a landscapes composed by highly fragmented forest patches interspersed in a matrix of agricultural ecosystems (Beasley and Rhodes 2010) demonstrated how raccoons modified their movement behaviour in response to the discontinuous nature of resources and suggested that the extent of raccoon space use in these ecosystems is strongly influenced by the availability and distribution of non-agricultural resources.

Edge permeability reflects the tendency of a disperser reaching the edge of a habitat patch to cross the boundary and emigrate. The understanding of the role of habitat edges in shaping the spatial behaviour of animals in fragmented terrestrial landscapes has led to different, sometimes opposite, results. In some cases, for example, when low-contrast edges become favoured foraging sites, bird species are described to benefit from fragmentation and enlarge their home range size to reach habitat edges (Marzluff et al. 2004 for Steller's Jays, *Cyanocitta stelleri*).

In other cases, fragmentation and the consequent increase in edge areas influence movement behaviour of species in an opposite way (i.e. avoidance of habitat edges), but with the same result of increasing the home range size: Hansbauer et al. (2008) revealed an edge avoidance behaviour of sensitive forest understory passerines in the fragmented Brazilian Atlantic Rainforest which increased the speed and distance they covered daily in order to reduce the higher predation risk they would be exposed to when foraging at habitat edges.

Conversely, when the edges of a habitat fragment are delimited by a barrier, evidence exists that animals somehow adapt the size and shape of home ranges to the size of the fragment. Small mammal movements can be easily stopped by habitat barriers like roads (Bakowski and Kozakiewicz 1988; Merriam et al. 1989) These barriers are not always absolute barriers, but can be effective inhibitors of movements, acting at the level of individual home ranges (Kozakiewicz 1993). Bakiwski and Kozakiewicz (1988) have found that 5m wide forest road acts as a quantitative barrier on bank voles (*Myodes glareoulus*) movements. Movements of voles across the road were infrequent, but almost all individuals translocated across the road returned back to their original side.

Thus, it appears that key factors affecting the size of the home ranges of animals in terrestrial fragmented landscapes are edge permeability and matrix quality (Andre 1994; Verbeylen et al. 2009). As explained above, in the case of the Tagliamento islands this edge is not a barrier but it is a high contrast edge which animals are able to cross. Indeed, *A. agrarius* was found to cross this edge in the time-span of a single radio-tracking session (10 days) and also trapping revealed inter-island movements: average inter-island distance moved by *A. flavicollis* was 290m ± 91 (N=5) and of 243m ± 107 (N= 10) for *A. sylvaticus*. Such distances appear quite large in comparison to other studies on movements of *A. flavicolli*s and *A. sylvaticus* using trapping in continuous forest habitats (e.g. Baláž and Ambros 2012; Vukicevic-Radi et al. 2006: 140m for *A. flavicollis*, 20m for *A. sylvaticus*). It could therefore be expected that not only *A. agrarius* but also individuals of *A. flavicollis* and *A. sylvaticus* would enlarge their home-ranges when moving on the islands and in the surroundings.

These results are not therefore in line with the predictions of island biogeography regarding the spatial behaviour of insular species, i.e. smaller home ranges of animals inhabiting islands in respect to their mainland counterparts. They do however fit perfectly into previous evidence regarding the factors affecting spatial behaviour of animals, i.e. home ranges are larger where food resources and density of competitors are lower. This happens in the study area on the islands, showing therefore an inverse trend in respect to a mainland-oceanic island system, but fitting with demonstrated tendences of animals inhabiting patchy terrestrial landcapes to enlarge their home ranges (as a consequence of patchy distribution of resources), if remnant habitat patches in the landscape are characterised by permeable edges and surrounded by a permeable matrix.

7.4 Reduction of predator species

Force of predation on islands has been shown to be less intense than on the mainland due to incomplete colonisation of islands by predators and because prey abundance and space are in general more limited (Foster 1964; Lomolino 2005). As a consequence the predator pressure exerted on small mammals on islands is in general lower (Adler and Levins 1994). In the Tagliamento riparian mosaic, mainland and islands seem to host an equally diverse community of predators, however the seasonal use of islands by predators varies throughout the year. Potential predators of mice in the study area were represented by carnivores and birds of prey. The impact of the latter on mice might be higher on large islands than on the mainland, given that results of this thesis indicate significant lower values of tree cover on large islands in respect to the mainland (see chapter 5, Figure 5.7). As for the smaller islands, the impact of birds of prey could be even more intense, since small islands have more sparse vegetation with respect to large islands, therefore making it easier for raptors to locate prey during their flights.

Carnivore species richness did not differ between mainland and islands (see chapter 2, section 2.5, Table 2.3). Moreover, results of this thesis indicate that the visiting rate of the most common carnivore species in the study area was in general lower on islands than on the mainland in each of the investigated seasons for *M. foina* and in spring mostly for *V. vulpes* (the other seasons having comparable visiting rates for this species; (see chapter 6, section 6.3.1, Table 6.1*):* Islands were seldom visited by *M. foina* and the peak visiting rate of this species was in autumn, in correspondence of the juveniles' dispersal. This would lead to a hypothesis that the carnivore predator pressure exercised by carnivores on small mammal populations was lower on the islands than on the mainland, as already observed in studies of island biogeography (e.g. Michaux et al. 2002). This hypothesis would not be in accordance with the exploratory results of chapter 6, where it emerged that small mammal abundance was not a variable driving the use *M. foina* makes of the islands of the Tagliamento. But the occurrence on a habitat island of a carnivore like *M. foina* is not necessarily a surrogate for a measure of predator pressure exerted on a community of *Apodemus*. However, the detected difference in the visiting rate of carnivores between the mainland and the islands of the Tagliamento would find confirmation to previous observed trends found in the US, where natural and artificial river islands have been widely recognized as a refuge for ground-nesting waterfowls and geese, because they are usually characterized by the absence or reduced occurrence of mammalian predators visiting them (Giroux 1981; Moser and Ratti 2005; Zoellick et al. 2004).

7.5 Changes in life history traits

7.5.1 Increased densities on islands

In insular populations of birds, excess density compensation and density compensation have been shown to occur and both are thought to be result of some form of niche expansion in the absence of competitors (MacArthur et al. 1972). On the other hand, through controlled introduction experiments of competitive rodent species, Crowell (1983) was able to demonstrate that increased densities in insular populations of *Myodes gapperi*, *Peromyscus maniculatus* and *Microtus pennsylvanicus* were not a result of niche-expansion and competitive release, but were attributable to the effects of restricted dispersal (and therefore to 'fence effect') in combination with predator release.

This study on the Tagliamento was able to demonstrate that just *A. sylvaticus* reached higher densities on islands with respect to the mainland, while the other two species showed opposite density patterns. As already widely discussed in section 7.2, density compensation, as a consequence of competitor release and of larger niche and adaptability of the generalist *A. sylvaticus*, is the most likely mechanism explaining these density trends, given that conditions for the fence effect do not apply to the Tagliamento river islands, at least in those periods of the year when flooding does not occur.

7.5.2 Decreased reproductive output on islands

Spatial density patterns for the three species did not result in predicted inverse patterns in their reproductive output. Number of reproductive females was lower on islands for *A. flavicollis* and *A. agrarius*, while significant differences were not found between mainland and islands for *A. sylvaticus.* According to the theory of island syndrome,an increase in density of insular small mammals corresponds to a decrease in their reproductive output (Adler and Levins 1994).

Studies that focus on demographic processes that determine how species respond to fragmentation provide contradictory results. For example, it has been shown that a reduction of available habitat to small mammals following fragmentation can have variable effects on reproductive rate. Wolff et al. (1997) monitored the short-term behavioural and demographic responses of gray-tailed voles (*Microtus canicaudus*) to the reduction and fragmentation of their available habitat through an experiment in enclosures. They found that a 70% reduction in habitat did not adversely affect the reproductive rate of voles. Conversely, Diffendorfer et al. (1995) compared number of reproductive females of small mammals in continuous versus fragmented old-field habitats in Kansas. The species under study were the hispid cotton rat (*Sigmodon hispidus*), the prairie vole (*Microtus ochrogaster*) and the deer mouse (*P. maniculatus*). They found higher proportions of reproductive females for *S. hispidus* and *M. ochranogaster* in continuous vs. fragmented habitats. Similarly, Holland and Bennet (2010) censused and compared reproductive traits of bush rat (*Rattus fuscipes*) in two large (49 ha) and eight small (2.5 ha) forest fragments in an agricultural region of south-eastern Australia. They found a positive significant interaction between the proportion of females breeding and fragment size, i.e. proportion of reproductive females was higher in large fragments than in small ones. These differences in life histories between continuous and fragmented habitats or between large and small habitat islands are discussed by the authors of the above cited studies as being related to a decrease in the carrying capacity of a habitat as a consequence of habitat fragmentation (Wolff et al. 1997). Going into more detail, the increased habitat area coupled with increase in quantity and quality of resources (and therefore reduced potential competition) in continuous areas vs. fragmented areas or in large habitat vs. small habitat islands, are reflected in higher percentage of reproductive females. Indeed, while male small mammals range widely during the breeding season, females are resident and depend on a high quality territory in which to rear their young (Wolff 1993).

It may therefore be suggested that the decreased reproductive output observed for *A. flavicollis* and *A. agrarius* on the islands of the Tagliamento (which did not correspond to an increased density in these habitats, as predicted by the theory of island syndrome) was due to the general less favourable conditions found for these two specialist species on the islands. As for *A. sylvaticus*, reproductive output did not differ between the mainland and islands, therefore confirming its extremely high adaptability to different environmental conditions.

7.5.3 Inter-specific relationships

Montgomery (1980; 1981) studied the mechanisms of competition between *A. flavicollis* and *A. sylvaticus* in continuous woodland habitats where the two species coexisted in the UK. The author showed that the two species can modify the length of the breeding season and their survival in conditions of sympatry. Moreover, by removing alternatively one of the two competitor species from two different trapping grids where they coexisted, he found that in the absence of their congener, both of them made greater use of areas woodland once frequented by the absent species and concluded that *A. sylvaticus* and *A. flavicollis* compete for space. Their interactions appeared not to strong enough to lead to complete exclusion from habitats where the two species coexisted.

Similar results of spatial segregation between these two species were revealed in a highly fragmented landscape of central Italy represented by woodland patches interspersed in an agricultural matrix (Sozio et al. 2015): *A. sylvaticus* and *A. flavicollis* partially segregated in different woodland patches according to patch quality, cover and connectivity.

As for *A. agrarius*, it is has been shown to be a species subordinate to the other two, whose population dynamics are strongly affected by the other *Apodemus* species present in the community (Gliwicz 1984). According to Gurnell (1985), *A. sylvaticus* and *A. agrarius* are quite similar in many respects and especially in their being subordinate to *A. flavicollis*. Moreover, in habitats where *A. agrarius* co-occurred with *A. flavicollis*, it showed higher mortality and emigration rates and lower survival of offspring (Gliwicz 1981).

Results obtained from chapter 4 strongly fit into these findings and are in support of the existence of mechanisms of inter-specific competition amongst the three mice species in the study area. *A. flavicollis* is the dominant species amongst the three (Gliwicz 1981). *A. sylvaticus* on the other hand is the most adaptable, being a generalist and can find refuge on islands. *A. agrarius* finds itself squeezed between these two species, not having the ability to compete with *A. flavicollis* based on size and in spite of being larger (see chapter 4, section 4.3.1, Figure 4.4) than *A. sylvaticus* cannot compete with this species on islands because this habitat does not sufficiently satisfy its food requirements. Although being extremely adaptable, *A. sylvaticus* on the mainland would suffer more competition with the other two *Apodemus* species because of their increased densities and reproductive output (see chapter 4, section 4.3.1, Figures 4.1 and 4.3).

Pavanello (2010) found the identical results in the same study area of the Tagliamento by trapping the same species the year before the fieldwork reported in this thesis started. In particular as a confirmation of the existence of a mechanism of competition between individuals of *A. agrarius* and *A. flavicollis* in the study area, the author found that on the mainland, where *A. agrarius* and *A. flavicollis* coexisted in relatively high densities, the two species were spatially segregated at microhabitat level given that they were seldom captured in the same traps.

The real existence of mechanisms of interspecific competition at population level between the three species on the Tagliamento should be confirmed through analysis directly measuring specific life history variation in *A. flavicollis* (and of *A. agrarius*), like survival or body weight, as function of the density of *A. sylvaticus* in the two habitats, i.e. on the mainland and on the islands. While it was not possible to analyse data on survival given the long time span between different trapping sessions (i.e. more than two months and the low inter-session recapture rates, see below) analysis of life history variation on islands (chapter 4) revealed that all the three species showed a decreased body weight and reproductive output on islands. Given the low sample size of the investigated sites (N=10 islands, N=3 mainland sites) it was not possible to model or correlate the reproductive output and body weight of *A. agrarius* and *A. flavicollis* as a function of the density of *A. sylvaticus* in the two habitats and therefore to confirm the existence of a pure mechanism of release from competitive pressure of *A. sylvaticus* on islands.

7.5.4 Increased survival on islands

Increased survival has been shown in several insular populations of small mammals (Adler and Levins 1994). Higher survival on islands was described as being the result of (1) more sedentary life style (no or reduced migration of individuals from and to islands), and increased tolerance of conspecifics (by selecting for decreased intra-specific aggressiveness) due to higher densities on islands (Crowell 1983; Knell 2009). The estimation of survival of small mammals was not feasible in this thesis, given that very few animals were recaptured in between different trapping sessions (inter-seasonal recapture rates: 13% for *A. flavicollis* and *A. agrarius*, 15% for *A. sylvaticus*) therefore it was not possible to test whether at least the only species which showed increased densities on river islands (*A. sylvaticus*) showed also increased survival.

7.5.5 Data collection for estimating life histories

In this thesis, data used for evaluating differences in life history traits of *Apodemus* species between mainland and island populations were collected once per season over one year. They therefore provide just a one-year snap-shot in the population dynamics of small mammal species living in the floodplain of the River Tagliamento. Periodic fluctuations in numbers of small rodents have been known for a very long time, at least in Northern Europe. As an example, population cycles of *Apodemus* species have been shown to last 3-6 years in Sweden (e.g. Bergstedt 1965; Marcstrom et al. 1990). Cyclic population dynamics of small mammals are not restricted to the boreal and arctic zones of Eurasia, but long-term data series from lower latitudes are less common and non-cyclic dynamics are indeed more common at lower latitudes. For example, a recent study carried out in eastern Poland using 22-year (1986–2007) trapping data from marginal meadow and river valley grasslands, showed that population dynamics of *A. agrarius* were not cyclic (Zub et al. 2012). Similarly, Gliwicz (1988) studied dispersal in a population of *A. flavicollis*, whose density was relatively stable over four years. In contrast, Wendland (1981) in

Germany, analysing trapping data for 28 years, found that significant changes in density were established for *A. flavicollis* at three-year intervals.

Results obtained over a one-year trapping campaign by Pavanello (2010) in the same study area, revealed similar patterns in the distribution of the three species of *Apodemus* across the Tagliamento mosaic. Moreover, seasonal variation of the capture rates of the three species he detected over one year, were also rather similar to the results presented here for the whole study period. In this study, *A. sylvaticus* was the most abundant species on the islands and number of trapped individuals over the whole study period decreased from May 2010 (spring session) to September (2010) (summer session) and then increased progressively in numbers from November 2010 (autumn session) to January 2011 (winter session). *A. flavicollis* was the most abundant species on the mainland and decreased progressively in numbers from May 2010 to January 2011. *A. agrarius* was the species captured with the lowest abundances in both habitats and after an increase in the number of trapped individuals between May 2010 and September 2010, its abundance decreased progressively until January 2011. Pavanello's results for variation in community composition between the mainland and the islands were exactly the same and results for seasonal trends of *A. agrarius* and *A. sylvaticus* provided identical trends. What differed in his work was an increasing trend for *A. flavicollis* between spring and summer trapping sessions, whereas this study found a decreasing trend in the same time-span. These similar results within two following years for all the three species are strongly in support for the validity of the observed species distributional patterns and competitive interactions explained in detail in the above sections.

7.6 Changes in body size

Trends in body-size of *Apodemus* spp. on the Tagliamento floodplain did not resemble patterns described elsewhere for insular small mammals according to the island rule (Foster 1964; Michaux et al. 2002), i.e. larger body size was not found for animals living on islands in respect to their mainland counterparts for any of the three species. Larger body sizes on oceanic islands are often attributed to reduced competitive and predatory pressures and to differences in productivity and availability of resources (Lomolino 2005).

Although studies on the morphological effects of fragmentation are relatively rare (Sarre 1995), some recent studies report significant morphological differences between vertebrate populations inhabiting fragments and those inhabiting more continuous stands of native habitats. For example, the abundance of prickly forest skinks (*Gnypetoscincus queenslandiae*) in Australia is lower in fragments of native rainforests, and individuals inhabiting these fragments are smaller than those in nearby continuous forests (Sumner et al. 1999). In addition, Schmidt and Jensen (2005) report changes in body size of Danish mammals and birds in response to landscape transformation in Denmark within comparatively short periods of time (e.g., 175 years). The nature of the size changes (increases or decreases) varied among species, but was consistent with general patterns of body-size evolution of vertebrates on islands (i.e., the island rule; Lomolino et al. 2005): small species of birds and mammals tended to increase in size and larger species tended to decrease in size. Similar trends were obtained by Holland and Bennet (2010) in Australia for the bush rat (*R. fuscipes*). The authors found that body weight of reproductive females of this species covariated positively with the area of the woodland patch where they were trapped.

In terrestrial landscapes, the relation between a decreased body size of animals inhabiting patchy habitats and those inhabiting continuous habitats has been attributed mainly to differences in the amount of resources found in the two habitat types. Lomolino and Perault (2007) analysed patterns in intraspecific body weight variation of small mammals across the fragmented, temperate rainforest landscapes of Washington State (USA) to test the hypothesis that creation of a mosaic of natural and anthropogenic habitats (i.e. old-growth continuous forests, old-growth forest fragments, old-growth corridors, clear-cuts and second-growth forest fragments) altered the body size of resident small mammals (*Sorex* spp, *Peromyscus* spp and *Clethrionomys* spp.). By comparing body weight of small mammals between large portions of continuous rainforest (i.e. mainland sites) with body weight of animals inhabiting old-growth fragments, the authors found weights of *S. trowbridgii*, *S. monticolus* and *P. keeni* were lower in old-growth fragments in respect to the mainland sites. These differences were discussed as being a consequence of spatial and environmental characteristics of the old-growth forest fragments as compared to the mainland sites: in addition to being by definition smaller and more isolated, the fragments had more open canopies, tended to be less humid than mainland forests and had a higher proportion of habitat edges than the continuous forest mainland.

Similar trends were also found more recently in amphibians. Steinicke et al. (2015) investigated the differences in body size and body weight in a habitat specialist frog (*Ischnocnema guentheri)* between continuous portions of the Atlantic Forest of south-eastern Brazil (control site) and small forest fragments. The effects of fragmentation on size and body condition of the frog were evident. They observed a lower body weight of the species in the smallest and more isolated forest fragments. This result was discussed as being a consequence of the lower quality of food resources and higher physiological stress (which translated into higher energetic costs) for the individuals inhabiting small fragments in respect to those inhabiting the control sites.

The observed trends in reduction of body weight found for all three *Apodemus* species studied on the Tagliamento reflects the findings for other species of small mammals and amphibians inhabiting fragmented terrestrial landscapes. Unlike results obtained for oceanic islands, where changes in body size and weight are attributed mainly to complex mechanisms of release from competition or from predator pressure, results from this thesis more closely align with explanations linked to differences in food resource availability found between the mainland and the islands and between different size categories of islands (see chapter 4, section 4.3.2, Figure 4.6 and chapter 5, section 5.3.3, Figure 5.7).

7.7 Conclusions

Seven of the 11 tenets that Adler and Levins (1994) and Vicente (1999) list as island phenomena have been studied in the context of river islands along the River Tagliamento and of these, four were found to follow predictions, two were not and one was uncertain (Table 7.1). The ones that did not follow the predictions (i.e. lack of a sedentary behaviour on islands and lack of an increase body size on islands) were tenets that required a similar or greater abundance of resources on islands, which is often the case on oceanic islands but not on the river islands of the Tagliamento.

Table 7.1 Trends and modifications in oceanic island communities as listed by Adler and Levins (1994) and Vicente (1999). Crossed cells indicate if they were considered in this thesis, empty cells indicate traits which were not taken into consideration and therefore which should be the object of further investigations. The last column resumes whether the findings of this thesis on the river islands of the Tagliamento reflect the trends described by Adler and Levins (1994) and Vicente (1999).

Trends observed in oceanic island communities	***Trend analysed on the Tagliamento***	***Trend observed on the Tagliamento***
Reduction of species diversity	☒	Yes
Over-representation of small generalists with large niches	☒	Yes
Enlargement of the niche	☐	
Sedentary behaviour	☒	No
Reduction of predator pressure	☒	Uncertain
Increment in density	☒	Yes
Decrement of reproductive output	☒	Yes
Increment of survival	☐	
Greater body size	☒	No
Genetic divergences	☐	
Reduced intraspecific aggression	☐	

Two tenets following the insular biogeography predictions were interlinked, i.e. the over-representation of the most generalist species (i.e. *A. sylvaticus*) resulted in this species being the most abundant on islands, mainly because generalists are extremely adaptable and have been proven to thrive in patchy terrestrial landscapes worldwide. The reduction in reproductive output was not a consequence of the increased densities of all three focal species on islands, but was again linked to a generally lower abundance of food resources on islands. Finally, the relationship between small mammal diversity and spatial attributes of islands observed in oceanic islands and very often also in habitat islands, resulted in a match in the observed positive relationship between species diversity and area of river islands, but not between species diversity and island isolation.

The findings of this thesis indicate that the islands on the River Tagliamento increase the level of habitat heterogeneity of the whole system for the *Apodemus* spp. community even though they are a lower-quality and a periodically disturbed habitat. Unlike oceanic islands and the nearest mainland, the mainland-island system of the Tagliamento is a much more inter-connected system that is likely to have a higher rate of emigration and immigration between these two habitats, resulting in a dilution of the effects that are commonly observed on oceanic islands. River islands of the Tagliamento would be therefore more similar to what has been defined in this thesis as habitat islands.

The fact that some of the insular trends were not observed (Table 7.1) is probably due to several different reasons: (1) the matrix surrounding these islands is not completely impermeable to any of the species that are the object of this study; (2) the relative closeness of the mainland to the river islands investigated here; and (3) the flooding dynamics of the river which could periodically reset the density and the species richness of small mammal communities on islands. These three peculiarities of the system under study are probably responsible for the lack of some of the predicted insular trends.

Some of the islands under investigation on the Tagliamento, in particular large islands (which can reach higher elevations on the gravel bars due to sediment deposition) may experience temporarily increased isolation during flood events, when they are surrounded by water. Therefore, further studies are needed to compare the dynamics of small mammals on these islands in the period in between floods with those during a flood. This would help to detect probable temporal crowding and fence effect mechanisms on islands.

In light of the findings of this thesis, there are some other areas that warrant further research and that would further confirm the discussed findings (Table 7.1). A study on the diet of the three *Apodemus* species should be carried out in the future to evaluate the width of their niche on the mainland and on islands. Finally, a study evaluating the genetic distance of different species of *Apodemus* between the mainland and islands and in-between distant islands would provide information on the permeability of the matrix for the movements of different species, and the connectivity of meta-populations.

7.7.1 The Tagliamento as model ecosystem of European importance

The 'habitat heterogeneity hypothesis' is one of the corner-stones of ecology (e.g. MacArthur and Wilson, 1967; Simpson, 1949). It assumes that structurally complex habitats may provide more niches and diverse ways of exploiting the environmental resources and thus increase species diversity (Bazzaz, 1975). Tews et al. (2004) performed a meta-analysis of studies examining the relationship between habitat heterogeneity and mammal species diversity and found that that, out of the 15 examined studies, ten proved the existence of a positive effect of habitat heterogeneity on mammal species diversity (e.g. Ecke et al. 2002, Williams et al. 2002), one showed no effect (Heaney et al. 2000) and three showed that an increased habitat heterogeneity caused a decrease in mammal species diversity (e.g. Sullivan et al 2000). In their review, Tews et al. (2004) underlined that the ecological effects of habitat heterogeneity may vary considerably between species groups depending on whether structural attributes are perceived as heterogeneity or fragmentation and discuss that negative effects of habitat heterogeneity may occur as a consequence of landscape fragmentation, causing the disruption of key biological processes such as dispersal and resource acquisition (Saunders et al. 1991).

The spatial heterogeneity of the Tagliamento is natural and is mainly maintained by the flood dynamics and by flows of mineral and organic matter, creating a complex shifting mosaic of river islands over a large spatial and temporal scale. Floods destroy older islands and create new ones resulting in an annual redistribution and sorting of sediment sizes, vegetation communities and new channel configurations (Tockner et al. 2003). Within the context of the findings of this thesis this dynamism, on the one hand periodically resets the small mammal diversity of islands on a local scale, but on the other hand creates spatial heterogeneity in the form of clusters of island habitats which allows for the rich community of small mammals to segregate, hence increasing small mammal species diversity at the landscape level. Despite being similar to a fragmented landscape, in that the floodplain is made by habitat islands interspersed in a gravel matrix, key biological processes for small mammals like resource acquisition and dispersal are not completely disrupted on river islands of the Tagliamento. Indeed, small mammal species may be able to reach high density on islands (*A. sylvaticus*), to move between islands and to reproduce on islands, with different efficiency dictated by their specialist or generalist habits.

The preserved natural geomorphological characteristics of the Tagliamento floodplain and its conserved natural flooding dynamics have served to define it as a model ecosystem of European importance also in view of their consequences on the biological communities present in the riverine mosaic (Tockner et al. 2003). Studies on animal populations inhabiting or using the Tagliamento riverine mosaic have shown that diversity of amphibians and insects is high and that communities of these two taxa show a differentiation in their relative species compositions between the riparian forest and the other habitats of the floodplain (e.g. water channels, islands, ponds, woody debris, etc) (Karaus et al. 2013; Langhans and Tockner 2014; Rust et al. 1998; Tockner et al. 2006). Similar results were obtained also for plants (Edwards et al. 1999; Francis et al. 2008). The important and interesting results presented in this thesis are complementary to these previous studies and therefore help with the establishment of the Tagliamento as a reference system by providing information on how small mammals use the riverine mosaic.

7.8 References

Adler, G.H. and Levins, R., 1994. The island syndrome in rodent populations, In The Quartely Review of Biology. pp. 473-490.

Amarasekare, P., 2003.Competitive coexistence in spatially structured environments: A synthesis. Ecology Letters 6, 1109-1122.

Andren, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. Oikos 71, 355-366.

Bakowski, C. and Kozakiewicz, M., 1988. The effect of forest road on bank vole and yellow-necked mouse populations. Acta theriologica 33, 345-353.

Baláž, I. and Ambros, M., 2012. Population analysis and spatial activity of rodents in flooded forest conditions. Ekologia Bratislava 31, 249-263.

Bazzaz, F.A. (1975) Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology 56, 485–488.

Beasley, J.C., Rhodes, O.E., 2010. Influence of patch- and landscape-level attributes on the movement behavior of raccoons in agriculturally fragmented landscapes. Canadian Journal of Zoology 88, 161-169.

Bergstedt, B., 1965. Distribution, reproduction and Dynamics of the rodent species Clethrionomys glareouls (Schreber), Apodemus flavicollis (Melchior) and Apodemus sylvaticus (Linne') in Southern Sweden. Oikos 16, 132-160.

Bolger, D.T., Alberts, A.C., Sauvajot, R.M., Potenza, P., Mccalvin, C., Tran, D., Mazzoni, S., Soulé, M.E., 1997. Response of rodents to habitat fragmentation in coastal southern California. Ecological Applications 7, 552-563.

Bossart, J.L., Opuni-Frimpong, E., Kuudaar, S., Nkrumah, E., 2006. Richness, abundance, and complementarity of fruit-feeding butterfly species in relict sacred forests and forest reserves of Ghana. Biodiversity and Conservation 15, 333-359.

Charles, J.K. and Ang, B.B., 2010. Non-volant small mammal community responses to fragmentation of kerangas forests in Brunei Darussalam. Biodiversity and Conservation 19, 543-561.

Collinge, S. K. 1995. Spatial arrangement of patches and corridors in the landscape: consequences for biological diversity and implications for landscape architecture. Ph.D. dissertation. Harvard University, Cambridge, Massachusetts.

Crowell, K.L., 1983. Islands - Insight or Artifact?: Population Dynamics and Habitat Utilization in Insular Rodents. Oikos 41, 442-454.

De La Sancha, N.U., 2014. Patterns of small mammal diversity in fragments of subtropical Interior Atlantic Forest in eastern Paraguay. Mammalia 78, 437-449.

Debinski, D.M. and Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14, 342-355.

Diaz, M., Santos, T., Telleria, J.L., 1999. Effects of forest fragmentation on the winter body condition and population parameters of an habitat generalist, the wood mouse Apodemus sylvaticus: a test of hypohtesis. Acta Oecologica 20, 39-49.

Diffendorfer, J.E., N.A. Slade, M.S. Gaines, Holt, R.D., 1995. Population dynamics of small mammals in fragmented and continuous old-field habitat. In W. Z. Lidicker Jr. (ed.), Landscape Approaches in Mammalian Ecology and Conservation. University of Minnesota Press, pp. 175-199.

Ecke, F., Lofgren, O., Sorlin, D., 2002. Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. Journal of Applied Ecology 39, 781–792.

Edwards, P.J., Kollmann, J., Gurnell, A.M., Petts, G.E., Tockner, K., Ward, J.V., 1999. A conceptual model of vegetation dynamics on gravel bars of a large Alpine river. Wetlands Ecology and Management 7, 141-153.

Forman, R.T.T. and Godron, M., 1981. Patches and structural components for a landscape ecology. BioScience 31, 733-740.

Francis, R.A., Tibaldeschi, P., McDougall, L., 2008. Fluvially-deposited large wood and riparian plant diversity. Wetlands Ecology and Management 16, 371-382.

Fox, B.J. and Fox, M.D., 2000. Factors Determining Mammal Species Richness on Habitat Islands and Isolates: Habitat Diversity, Disturbance, Species Interactions and Guild Assembly Rules. Global Ecology and Biogeography 9, 19-37.

Foster, B.L., 1964. Evolution of mammals on islands. Nature 202, 234-235.
Giroux, J., 1981. Use of artificial islands by nesting waterfowl in southeastern Alberta. Journal of Wildlife Management 45, 669-679.

Gascon, C., Lovejoy, T.E., Bierregaard Jr., R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S., 1999. Matrix habitat and species richness in tropical forest remnants. Biological Conservation 91, 223-229.

Giroux, J., 1981. Use of artificial islands by nesting waterfowl in southeastern Alberta. Journal of Wildlife Management 45, 669-679.

Gliwicz, J., 1981. Competitive interactions within a forest rodent community in central Poland. Oikos 37, 353-362.

Gliwicz, J., 1984. Competition among forest rodents: effects of apodemus flavicollis and clethrionomyis glareolus on A. agrarius. Acta Zoologica Fennica 172, 57-60.

Gliwicz, J., 1988. Seasonal dispersal in non-cyclic populations of Clethrionomys glareolus and Apodemus flavicollis. Acta Theriologica 33, 263-272.

Goodman, S.M. and Rakotondravony, D., 2000. The effects of forest fragmentation and isolation on insectivorous small mammals (Lipotyphla) on the Central High Plateau of Madagascar. Journal of Zoology 250, 193-200.

Gurnell, J., 1985. Woodland rodent communities. Symposia of the Zoological Society of London 55, 377-411.

Hanley, T.A. and Barnard, J.C., 1999. Spatial Variation in Population Dynamics of Sitka Mice in Floodplain Forests. Journal of Mammalogy 80, 866-879.

Hanser, S.E. and Huntly, N.J., 2006. The biogeography of small mammals of fragmented sagebrush-steppe landscapes. Journal of Mammalogy 87, 1165-1174.

Hansbauer, M.M. and Storch, I., Leu, S., Nieto-Holguin, J.-P., Pimentel, R.G., Knauer, F., Metzger, J.P.W., 2008. Movements of neotropical understory passerines affected by anthropogenic forest edges in the Brazilian Atlantic rainforest. Biological Conservation 141, 782-791.

Hansson, L., 1985. The food of bank voles, wood mice and yellow necked mice. Symposia of the Zoological Society of London 55, 141-168.

Harcourt, A.H. and Doherty, D.A., 2005. Species-area relationships of primates in tropical forest fragments: A global analysis. Journal of Applied Ecology 42, 630-637.

Hare, E., 2009. Island syndrome in rodents: a comparative study on island forms of the bank vole, Myodes glareolus. PhD Thesis, School of Biological Sciences, Queen Mary University London, UK.

Harris, J.H. and Leitner, P., 2004. Home-range size and use of space by adult mohave ground squirrels, Spermophilus mohavensis. Journal of Mammalogy 85, 517-523.

Heaney, L.R., 2001. Small mammal diversity along elevational gradients in the Philippines: An assessment of patterns and hypotheses Global Ecology and Biogeography 10, 15-39.

Holland, G.J., Bennett, A.F., 2010. Habitat fragmentation disrupts the demography of a widespread native mammal. Ecography 33, 841-853.

Johnstone, C.P., Lill, A., Reina, R.D., 2011. Response of the agile antechinus to habitat edge, configuration and condition in fragmented forest. PLoS ONE 6, art. no. e27158.

Jonsson, P., Hartikainen, T., Koskela, E.S.A., Mappes, T., 2002. Determinants of reproductive success in voles: Space use in relation to food and litter size manipulation. Evolutionary Ecology 16, 455-467.

Karaus, U., Larsen, S., Guillong, H., Tockner, K., 2013. The contribution of lateral aquatic habitats to insect diversity along river corridors in the Alps. Landscape Ecology 28, 1755-1767.

Knell, R.J., 2009. Population density and the evolution of male aggression. Journal of Zoology 278, 83-90.

Kollmann, J., Vieli, M., Edwards, P.J., Tockner, K., Ward, J.V., 1999. Interaction between vegetation developement and island formation in the Alpine river Tagliamento., In Appl. veg. Sci., pp. 25-36.

Kozakiewicz, M., 1993. Habitat isolation and ecological barriers – the effects on small mammal populations and communities. Acta Theriologica 39, 1-30.

Kozakiewicz, M., Gortat, T., Kozakiewicz, A., Barkowska, M., 1999. Effects of habitat fragmentation on four rodent species in a Polish farm landscape. Landscape Ecology 14, 391-400.

Kozakiewicz, M., Gortat, T., Panagiotopoulou, H., Gryczyńska-Siemiątkowska, A., Rutkowski, R., Kozakiewicz, A., Abramowicz, K., 2009. The spatial genetic structure of bank vole (Myodes glareolus) and yellow-necked mouse (Apodemus flavicollis) populations: The effect of distance and habitat barriers. Animal Biology 59, 169-187.

Kuncova, P. and Frynta, D., 2009. Interspecific morphometric variation in the postcranial skeleton in the genus *Apodemus*. Belgian Journal of Zoology 139, 133-146.

Kupfer, J. A., Malanson, G. P., Franklin, S. B., 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation. *Global Ecology and Biogeography* 15, 8-20.

Langhans, S.D. and Tockner, K., 2014. Edge effects are important in supporting beetle biodiversity in a Gravel-bed river floodplain. PLoS ONE 9, art. no. e114415.

Lawlor, T.E., 1982. The Evolution of Body Size in Mammals: Evidence from Insular Populations in Mexico. The American Naturalist 119, 54-72.

Lomolino, M.V., 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32, 1683-1699.

Lomolino, M.V. and Smith, G.A., 2003. Prairie dog towns as islands: Applications of island biogeography and landscape ecology for conserving nonvolant terrestrial vertebrates. Global Ecology and Biogeography 12, 275-286.

Lomolino, M.V. and Perault, D.R., 2001. Island biogeography and landscape ecology of mammals inhabiting fragmented, temperate rain forests. Global Ecology and Biogeography 10, 113-132.

Lomolino, M.V. and Perault, D.R., 2007. Body size variation of mammals in a fragmented, temperate rainforest. Conservation Biology 21, 1059-1069.

MacArthur, R.H. and Wilson, E.O., 1967. The Theory of Island biogeography. Princeton University Press.

MacArthur, R.H. and Diamond, J.M., Karr, J.R., 1972. Density compensation in island faunas. Ecology 53, 330-342.

Magnus, L.Z. and Cáceres, N.C., 2012. Effects of area size on the species richness and composition of small mammals in the Atlantic Forest of Brazil Mastozoologia Neotropical 19, 243-258.

Marcstrom, V., Hoglund, N., Krebs, C.J., 1990. Periodic Fluctuations in Small Mammals at Boda, Sweden from 1961 to 1988. Journal of Animal Ecology 59, 753-761.

Marsh, A.C.W., Harris, S., 2000. Partitioning of woodland habitat resources by two sympatric species of Apodemus: Lessons for the conservation of the yellow-necked mouse (A. flavicollis) in Britain. Biological Conservation 92, 275-283.

Marzluff, J.M., Millspaugh, J.J., Hurvitz, P., Handcock, M.S., 2004. Relating resources to a probabilistic measure of space use: Forest fragments and Steller's Jays. Ecology 85, 1411-1427.

Merriam, G., Kozakiewicz, M., Tsuchiya, E., Hawley, K., 1989. Barriers as boundaries for metapopulations and demes of Peromyscus leucopus in farm landscapes. Landscape Ecology 2, 227-235.

Michaux, J.R., De Bellocq, J.G., Sarà, M., Morand, S., 2002. Body size increase in insular rodent populations: A role for predators? Global Ecology and Biogeography, 11, 427-436.

Michel, N., Burel, F., Butet, A., 2006. How does landscape use influence small mammal diversity, abundance and biomass in hedgerow networks of farming landscapes? Acta Oecologica 30, 11-20.

Montgomery, W.I., 1980. Spatial organization in sympatric populations of Apodemus sylvaticus (L.) and A. flavicollis (Rodemtia, Muridae). Journal of Zoology 192, 351-377.

Montgomery, W.I., 1981. A removal experiment with sympatric populations of Apodemus sylvaticus (L.) and A. flavicollis (Melchior) (Rodentia: Muridae). Oecologia 51, 123-132.

Moser, A.M. and Ratti, J.T., 2005. Value of riverine islands to nongame birds. Wildlife Society Bulletin 33, 273-284.

Negro, M., Isaia, M., Palestrini, C., Rolando, A., 2009. The impact of forest ski-pistes on diversity of ground-dwelling arthropods and small mammals in the Alps. Biodiversity and Conservation 18, 2799-2821.

Nupp, T.E. and Swihart, R.K., 2000.Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. Journal of Mammalogy 81, 512-526.

Nupp, T.E. and Swihart, R.K., 2001. Assessing competition between forest rodents in a fragmented landscape of midwestern USA. Mammalian Biology 66, 345-356.

Pardini, R., De Souza, S.M., Braga-Neto, R., Metzger, J.P., 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape Biological Conservation 124, 253-266.

Pardini, R., De Bueno, A.A., Gardner, T.A., Prado, P.I., Metzger, J.P., 2010. Beyond the fragmentation threshold hypothesis: Regime shifts. biodiversity across fragmented landscapes. PLoS ONE 5 art. no. e13666.

Pavanello, M., 2010. Studio delle comunita' di piccoli mammiferi in un ambiente naturale frammentato: le isole del fiume Tagliamento. MSc Thesis, Department of Life Sciences, Trieste University. In Dipartimento di Biologia. Trieste University.

Prevedello, J.A. and Vieira, M.V., 2010. Plantation rows as dispersal routes: A test with didelphid marsupials in the Atlantic Forest, Brazil. Biological Conservation 143, 131-135.

Relyea, R.A., Lawrence, R.K., Demarais, S., 2000. Home range of a desert mule deer: testing body size and habitat productivity hypothesis. Journal of Wildlife Management 64, 146-153.

Ricketts, T.H., 2001. The matrix matters: Effective isolation in fragmented landscapes. American Naturalist 158, 87-99.

Rosenblatt, D.L., Heske, E.J., Nelson, S.L., Barber, D.M., Miller, M.A., MacAllister, B., 1999. Forest fragments in east-central Illinois: Islands or habitat patches for mammals? American Midland Naturalist 141, 115-123.

Rosenzweig, M.L., 1995. Species diversity in space and time. Cambridge University Press, Cambridge.

Russildi, G., Arroyo-Rodríguez, V., Hernández-Ordóñez, O., Pineda, E., Reynoso, V.H., 2016. Species- and community-level responses to habitat spatial changes in fragmented rainforests: assessing compensatory dynamics in amphibians and reptiles. Biodiversity and Conservation 25, 375-392.

Rust, C., 1998. Die okologische Bedeutung von Inseln and Schotterbänken im Tagliamento (Friaul, Italien) am Beispiel del Laufkäferzőnose (carabidae, Insecta), Diplomarbeit, ETH-Zűrich.

Sale, M.G. and Arnould, J.P.Y., 2009. Spatial and temporal organization in the swamp antechinus: comparison between island and mainland populations. Journal of Mammalogy 90, 347-355.

Sarà, M., 2008. The use of artificial nest-boxes by Apodemus sylvaticus dichrurus in Sicily. Folia Zoologica 57, 294-299.

Sarre, S., 1995. Size and structure of populations of Oedura reticulata (Reptilia: Gekkonidae) in woodland remnants: Implications for the future regional distribution of a currently common species. Australian Journal of Ecology 20, 288-298.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5, 18-32.

Schmidt, N.M. and Jensen, P.M., 2005. Concomitant patterns in avian and mammalian body length changes in Denmark. Ecology and Society 10, art. no. 5, 8 p.

Schradin, C. and Pillay, N., 2006. Female striped mice (Rhabdomys pumilio) change their home ranges in response to seasonal variation in food availability. Behavioral Ecology 17, 452-458.

Silva, M., 2001. Abundance, diversity, and community structure of small mammals in forest fragments in Prince Edward Island National Park, Canada. Canadian Journal of Zoology 79, 2063-2071.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688.

Sozio, G. and Mortelliti, A., 2015. Empirical evaluation of the strength of interspecific competition in shaping small mammal communities in fragmented landscapes. Landscape Ecology, 15 p. Article in Press.

Steel, E.A., Naiman, R.J., West, S.D., 1999. Use of woody debris piles by birds and small mammals in a riparian corridor. Northwest Science 73, 19-26.

Steinicke, H., Gruber, B., Grimm, A., Grosse, W.-R., Henle, K., 2015. Morphological shifts in populations of generalist and specialist amphibians in response to fragmentation of the brazilian Atlantic forest. Nature Conservation 13, 47-59.

Stepankova, J. and Vohralik, V., 2009. Vertical activity of the yellow-necked mouse (Rodentia: Muridae) at edge of a mixed forest. Folia Zoologica 58, 26-35.

Stevens, S.M. and Husband, T.P., 1998. The influence of edge on small mammals: Evidence from Brazilian Atlantic forest fragments. Biological Conservation 85, 1-8.

Sullivan, T.P., Sullivan, D.S., Lindgren, P.M.F. , 2000. Small mammals and stand structure in young pine, seed-tree, and old-growth forest, southwest Canada. Ecological Applications 10, 1367-1383.

Sumner, J., Moritz, C., Shine, R., 1999. Shrinking forest shrinks skink: Morphological change in response to rainforest fragmentation in the prickly forest skink (Gnypetoscincus queenslandiae). Biological Conservation 91, 159-167.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. Journal of Biogeography 31, 79-92.

Tockner, K., Ward, J.V., Arscott, D.B., Edwards, P.J., Kollmann, J., Gurnell, A.M., Petts, G.E., Maiolini, B., 2003. The Tagliamento river: a model ecosystem of European importance. Aquatic Science 65, 239-253.

Tockner, K., Klaus, I., Baumgartner, C., Ward, J.V., 2006. Amphibian diversity and nestedness in a dynamic floodplain river (Tagliamento, NE-Italy). Hydrobiologia 565, 121-133.

Verbeylen, G., Wauters, L.A., De Bruyn, L., Matthysen, E., 2009. Woodland fragmentation affects space use of Eurasian red squirrels. Acta Oecologica, 94-103.

Vicente, L., 1999. Evolutionary strategies in insular environments. Natura Croatica 8, 301-323.

Vieira, M.V., Olifiers, N., Delciellos, A.C., Antunes, V.Z., Bernardo, L.R., Grelle, C.E.V., Cerqueira, R., 2009. Land use vs. fragment size and isolation as determinants of small mammal composition and richness in Atlantic Forest remnants. Biological Conservation 142, 1191-1200.

Vukicevic-Radi, O., Mati, R., Kataranovski,C., Stamenkovi, S., 2006. Spatial organization and home range of Apodemus flavicollis and A. agrarius on Mt. Avala, Serbia. Acta Zoologica Academiae Scientiarum Hungaricae 52, 81-96.

Youngentob, K.N., Yoon, H.-J., Coggan, N., Lindenmayer, D.B., 2012. Edge effects influence competition dynamics: A case study of four sympatric arboreal marsupials. Biological Conservation 155, 68-76.

Wendland, V., 1981. Cyclic population changes in three mouse species in the same woodland. Oecologia 48, 7-12.

Williams, S.E., Marsh, H.,Winter, J , 2002. Spatial scale, species diversity, and habitat structure: Small mammals in Australian tropical rain forest. Ecology 83, 1317-1329.

Wolff, J.O., 1993. Why are female small mammals territorial? Oikos 68, 364-370.

Wolff, J.O., Schauder, E.M., Daniel Edge, W., 1997. Effects of habitat loss and fragmentation on the behavior and demography of gray-tailed voles. Conservation Biology 11, 945-956.

Wolff, J.O., Barrett, G.W., 2008. Landscape ecology of the golden mouse. In: Barrett, G.W., Feldhamer, G.A. (eds). Ecology, Behaviour, and Conservation of the Golden Mouse: Ecology and Conservation, Springer, pp. 99-113.

Zoellick, B.W., Ulmschnelder, H.M., Cade, B.S., Stanley, A.W., 2004. Isolation of Snake river islands and mammalian predation of waterfowl nests. Journal of Wildlife Management 68, 650-662.

Zollner, P.A. and Lima, S.L., 1997. Landscape-level perceptual abilities in white-footed mice: Perceptual range and the detection of forested habitat. Oikos 80, 51-60.

Zollner, P.A. and Lima, S.L., 1999. Orientational data and perceptual range: Real mice aren't blind. Oikos 84, 164-166.

Zub, K., Jędrzejewska, B., Jędrzejewski, W., Bartoń, K.A., 2012. Cyclic voles and shrews and non-cyclic mice in a marginal grassland within European temperate forest. Acta Theriologica 57, 205-216.